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Consequences of Vegetation Change on the Dynamics of Labile Organic Matter and Soil Nitrogen Cycling in a Semiarid Ecosystem

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CONSEQUENCES OF VEGETATION CHANGE ON THE DYNAMICS OF LABILE ORGANIC MATTER AND SOIL NITROGEN CYCLING IN A SEMIARID ECOSYSTEM

by

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ABSTRACT

Consequences of Vegetation Change on the Dynamics of Labile Organic Matter and Soil Nitrogen Cycling in a Semiarid Ecosystem

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Sagebrush-dominated ecosystems are being transformed by wildfire, rangeland improvement techniques, and exotic plant invasions. These disturbances have substantial effects on the composition and structure of native vegetation, but the effects on ecosystem C and N dynamics are poorly understood. To examine whether differences in dominant vegetation affect the quantity and quality of plant organic matter inputs to soil, ecosystem C and N pools and rates of plant turnover were compared among historically grazed Wyoming big sagebrush, introduced perennial crested wheatgrass, and invasive annual cheatgrass communities. Since low soil moisture during the summer may inhibit the microbial colonization of plant detrital inputs and result in C-limitations to microbial growth, soils were treated with an *in situ* pulse of plant detritus prior to the onset of the summer dry-season, and rates of soil C and gross N cycling were compared between treated and untreated soils. Finally, because plant detritus is the dominant form of labile C input to soil microbes over a large portion of the year, the decomposition of ^{13}C-labeled

annual grass detritus was used to determine the importance of plant detritus versus soil organic matter as microbial substrate. Results revealed large differences in ecosystem C and N pools, and in the quantity of plant C and N inputs to soil among vegetation types, but differences in soil C and N cycling rates were more subtle. Plant biomass pools were greatest for sagebrush stands, but plant C and N inputs to soil were greatest in cheatgrass communities, such that rates of plant C and N turnover appeared to be accelerated in disturbed ecosystems. Earlier release of plant biomass to soil detrital pools stimulated N availability to a greater extent than C availability relative to untreated soils, and this effect could not be predicted from the C:N stoichiometry of plant detritus. Finally, *in situ* decomposition of cheatgrass detritus was rapid; however, there was no clear evidence of a time-lag during summer in microbial colonization of recently released plant detritus, and microbial consumption of plant detritus did not result in N-limitations to microbial growth.

(170 pages)

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CHAPTER 1

INTRODUCTION TO THE DISSERTATION RESEARCH

Decomposition of plant detritus by soil microorganisms is a key linkage between plant net primary production and nutrient cycling in terrestrial ecosystems. This process is driven by microbial consumption of organic matter in order to obtain nutrients and energy-rich substrates for growth. Strong feedbacks are expected between microbial activity and plant production in terrestrial ecosystems because plant detrital inputs are an importance source of labile C to microbes, and because microbial C dynamics ultimately result in the mineralization of nutrients required for plant growth. While it is relatively clear that rates of soil microbial growth and activity are regulated by both the availability of labile C and N substrates, and environmental conditions (e.g. soil temperature and moisture), it is not clear how these factors interact in semiarid ecosystems.

The research in this dissertation is focused on how microbial C and N dynamics are regulated by the quantity and quality of plant-derived organic matter inputs and by seasonal patterns in environmental conditions. This research was undertaken in a semiarid rangeland ecosystem in the eastern Great Basin that exhibits strong seasonal variation in environmental conditions and contains an extensive patchwork of distinct monodominant plant communities.

Sagebrush-dominated ecosystems occupy extensive land areas of the western U.S. (West and Young 2000), and are impacted by a variety of disturbances that typically cause a shift in plant dominance from shrubs to introduced perennial or invasive annual grasses (Stewart and Hull 1949, D'Antonio and Vitousek 1992, West 1999). Differences in plant biomass distribution and turnover among plant life-forms are likely to

significantly affect biogeochemical cycling. However, in spite of the extensive land area covered by semiarid ecosystems, there are surprisingly few data regarding the effects of vegetation change on rates of ecosystem C and N cycling in these ecosystems. Given that rates of plant primary production and soil organic matter decomposition are commonly limited by the availability of soil N for plant uptake, there is a strong need to better understand the factors that control soil C and N availability in these ecosystems.

Climate and vegetation in the Great Basin

The climate in semiarid areas of the Great Basin is characterized by cold winters and a pronounced summer dry season that restricts high rates of plant and microbial activity to spring and autumn, when soils are moist. Precipitation is distributed nearly evenly over the year (Figure 1-1), but soil water accumulation is restricted to the cooler autumn and winter months (Dobrowolski et al. 1990).

The natural vegetation of many semiarid Great Basin rangelands is dominated by stands of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), with native perennial grasses (*Pseudoroegneria spicata* and *Elymus elymoides*) occurring in the interspaces between shrubs. The introduced perennial crested wheatgrass (*Agropyron desertorum*) is commonly planted in these areas to improve rangeland forage potential. These perennial plants survive the summer dry season by maintaining deep root distributions and shedding leaf tissues (West and Fareed 1973, Noy-Meir 1973, Fernandez and Caldwell 1975, Comstock and Ehleringer 1992, Evans and Black 1993).

A growing concern in semiarid ecosystems is the expansion and dominance of the invasive annual cheatgrass, *Bromus tectorum* (Billings 1994, Pellant and Hall 1994, West

1999). In contrast to perennial vegetation, cheatgrass successfully avoids the summer dry season by rapid growth early in the spring, and initiation of senescence prior to the onset of summer dry season (Stewart and Hull 1949, Hulburt 1955, Harris 1967).

Differences in phenology among shrub, perennial grass, and annual grass vegetation types are likely to result in differences in the timing and rates of plant N uptake and biomass turnover (Comstock and Ehleringer 1992, Bilbrough and Caldwell 1997). For example, earlier spring growth of annual grasses may result in higher rates of plant N uptake compared to perennial plants. However, given the longer growing period of perennial grasses and shrubs, total plant growth (i.e. net primary production) and plant biomass may be greater than for annual grasses. There is currently little comparative data on total plant growth and nutrient content among distinct vegetation types occupying similar soils, especially in semiarid rangeland ecosystems. These factors are important in understanding whether, for example, cheatgrass invasion of sagebrush rangeland results in net ecosystem C loss, and whether changes in plant growth and nutrient cycling after vegetation change will result in either positive or negative feedbacks to ecosystem C storage over time.

Quantity and quality of plant detrital inputs to soil

In addition to differences in phenology, the distribution and turnover of plant above- and belowground biomass, and the efficiency of nutrient resorption during senescence are also likely to differ among plant life-forms (Killingbeck 1996, Gill and Jackson 2000, Schenk and Jackson 2002). These factors are directly related to the quantity and quality of plant organic matter inputs to soil, and have been reported to alter

soil C and N availability (Vinton and Burke 1995, Carrera et al. 2003). Increased C inputs, through greater foliage or root turnover, should stimulate microbial growth and microbial N demand (Hart et al. 1994, Gallardo and Schlesinger 1995, Schaeffer and Evans 2005), and therefore reduce N available for plant uptake. By contrast, increased quality of plant detrital inputs (i.e. lower C:N ratios) should increase N availability to plants, due to decreased microbial demand for inorganic N per unit of C consumed (Chen and Stark 2000, Saetre and Stark 2005). It is currently unclear whether vegetation change in the Great Basin affects the quantity and quality of plant detrital inputs to soil.

Seasonal interactions between climate and plant phenology

In semiarid ecosystems, interactions between climate and plant phenology may have substantial effects on temporal patterns of soil C and N availability. Plant growth appears to be limited by N availability when environmental conditions are adequate in spring (James and Jurinak 1978, Bilbrough and Caldwell 1997, Duke and Caldwell 2001). There is little information on the seasonal dynamics of microbial activity in soils from semiarid systems, but microbial activity has been observed to be limited by C or N availability (Gallardo and Schlesinger 1995, Schaeffer and Evans 2005), or both (Chen and Stark 2000). Rates of microbial activity have been linked to soil C availability across broad climate gradients (Zak et al. 1994, Barrett and Burke 2000, Booth et al. 2005), and beneath plant canopies versus plant-interspaces (Barrett and Burke 2000, Chen and Stark 2000), suggesting that supplies of labile C are a key factor controlling microbial growth. Currently, it remains unclear to what extent differences in plant life-form and phenology among semiarid vegetation types affect the availability of C and N to soil microbes.

Research in other ecosystems with strong seasonality suggests that rapid cycling of C and N may occur during periods when plants are not actively growing. For example, in a tropical savanna, soil inorganic N pools have been shown to increase during the dry season. Subsequently, the decrease in inorganic N during the wet-season could account for a large proportion of plant N uptake (Augustine and McNaughton 2004). Similarly, in an alpine meadow, microbial biomass N accumulated in conjunction with litter decomposition over winter, and was released as a pulse of plant available N during spring snow melt (Brooks et al. 1998, Schmidt and Lipson 2004, Schmidt et al. 2007). Since both the release of microbial N and the accumulation of inorganic N are expected to result from a C-limitation to microbial growth (Hart et al. 1994, Chen and Stark 2000), these studies reveal a strong temporal component to the availability of labile substrates to soil microbes. Large seasonal shifts in N- versus C-limitations to microbial activity may also be an important factor in the biogeochemical cycling of sagebrush-dominated ecosystems; for example, large seasonal variations in soil nutrient availability could offer windows of opportunity for the establishment of exotic plant species during time periods when native perennial plants are inactive.

The inconsistency of C inputs and NO_3^- accumulation in semiarid soils

There is some evidence that seasonal patterns of environmental conditions and plant phenology affect the temporal pattern of soil C and N cycling in semiarid ecosystems. As the summer dry season develops, annual grasses initiate senescence (Stewart and Hull 1949, Harris 1967), while perennial plants reduce growth rates, shed biomass, and shift the distribution of active roots to deeper soil depths (West and Fareed

1973, Fernandez and Caldwell 1975, Comstock and Ehleringer 1992, Evans and Black 1993). Thus, soil C availability would be expected to increase during the early summer due to the pulse of high C:N leaf and root litter inputs. However, surface soils of semiarid ecosystems have been observed to accumulate NO_3^- during the summer (Jones and Woodmansee 1979, Jackson et al. 1988), particularly in soils dominated by annual grasses (Booth et al. 2003, Sperry et al. 2006). Soil NO_3^- accumulation is typically considered evidence that microbial growth is C-limited, but this is inconsistent with the expectation that inputs of plant detritus should stimulate soil C availability. One explanation for this inconsistency could be that there are important, but presently unknown interactions among environmental conditions, microbial activity and decomposition of plant detritus in semiarid ecosystems. It is possible that, by the time of annual grass senescence in late spring (late-May to early-June), the soil is already too dry for microbes to colonize the newly released detritus. Thus, there may be a time-lag in N immobilization until soil moisture increases in autumn.

Controls on microbial C and N dynamics

The supply of plant C inputs to soil, through leaf and root turnover, is an important source of labile C substrate that drives the growth and activity of heterotrophic soil microorganisms. As microbial populations grow, nutrients (such as N) must be assimilated in order to maintain stoichiometric balance of the new biomass. Nitrogen may be obtained either from the substrate consumed by the microbe (as organic N), or immobilized from soil solution as inorganic N. Since the C:N ratios of plant detritus (20 to over 100:1) are greater than that of microbial biomass (5 to 9:1) (Smith and Paul 1990,

Schlesinger 1997), microbial consumption of plant detritus is expected to result in microbial immobilization of inorganic N from the soil solution, and this is expected to decrease N availability for plant uptake. In contrast, microbial consumption of organic matter with narrow C:N ratios should result in N mineralization.

The availability of labile C derived from decomposing detritus exerts a strong control over both the supply and demand of microbial N. At the scale of individual microbes, the balance of N mineralization versus N immobilization is primarily regulated by the amount of microbial biomass growth per unit substrate consumed (substrate use efficiency, SUE), and the C:N ratio of the substrate consumed (see Austin et al. 2004, Saetre and Stark 2005). The substrate use efficiency affects the microbial mineralization-immobilization balance by controlling the amount of substrate-C utilized to build new microbial biomass; greater SUE results in greater microbial N demand from both organic N and inorganic N sources. If there is insufficient organic N within the substrate to build new microbial biomass, then inorganic N must be immobilized from the soil solution. Microbial substrate use efficiency is expected to increase with greater substrate and nutrient availability, and higher quality substrates (del Giorgio and Cole 1998). However, the bulk of research on this topic has been done in aquatic systems and laboratory cultures; factors controlling SUE in soils under field conditions are poorly understood.

Depending on the microbial C:N ratio and substrate use efficiency, an increase in substrate C:N ratios could result in either a decrease in N mineralization, or an increase in N demand for inorganic N (immobilization). Unfortunately, the C:N ratio of substrates utilized by soil microbes cannot be measured directly, largely because of the complexity

of chemical compounds derived from plant detritus and soil organic matter (Paul and Clark 1996), and the uncertainty of substrate preferences of complex microbial communities. However, microbial substrate C:N ratios can be estimated by modeling microbial C and N dynamics (Saetre and Stark 2005). In the following section, I discuss the heterogeneity of soil organic matter and how this may affect our understanding of microbial C and N cycling processes.

Soil microbes inhabit distinct microsites based on substrate quality

The chemical characteristics and C:N stoichiometry of organic matter in soils are not homogeneous. Relatively undecomposed plant detritus, with high C:N ratios, accounts for only a small proportion of the total organic matter in soil (Schlesinger 1997, Six et al. 2001, Swanston et al. 2004). The vast majority of soil organic matter consists of more highly decomposed material that is chemically complex, has low C:N ratios, and may be chemically or physically protected from microbial attack (Christensen 2001, Crow et al. 2007). The heterogeneous distribution of organic matter may provide distinct microsites for soil microbes, characterized by C-rich (N-limited) and N-rich (C-limited) substrates (Chen and Stark 2000, Schimel and Bennett 2004).

The simultaneous occurrence of N mineralization and N immobilization in bulk soils provides support for the idea that microbial activity is heterogeneously distributed in distinct microsites (Chen and Stark 2000). Consumption of labile C results in microbial growth and immobilization of available N (Hart et al. 1994, Gallardo and Schlesinger 1995, Whalen et al. 2000, Schaeffer and Evans 2005). Simultaneously, in comparatively N-rich microsites, microbial intra- and extracellular enzyme activity and biomass

turnover result in the mineralization of actively cycled N (Bengtsson et al. 2003, Schimel and Weintraub 2003, Saetre and Stark 2005). While the source of mineralizable N is believed to be derived predominantly from older, more highly decomposed mineral-associated organic matter with narrow C:N ratios, such as the heavy fraction (HF), high rates of microbial N immobilization are believed to be associated with C-rich particulate organic matter derived from plant detritus, such as the light fraction (LF) (Sollins et al. 1984, Boone 1994, Crow et al. 2007). Physical fractionation of soil organic matter combined with stable isotope tracing may be a productive approach to understanding the controls on microbial C and N cycling within soil microsites.

Overview of research in this dissertation

The three research chapters in this dissertation may be broadly viewed within a hierarchical structure, and contribute to understanding how the timing, quantity and quality of plant detrital inputs to soil affects key components of biogeochemical cycling in semiarid ecosystems. In the first chapter I report on a comparison of the distribution and cycling of ecosystem C and N among three distinct semiarid vegetation types (*Chapter 2*). Next, I compare soil C and N cycling rates in response to a springtime pulse of plant detritus (*Chapter 3*). And finally, I examine differences in microbial utilization of substrates derived from recent plant detritus versus substrates derived from older, more highly decomposed soil organic matter during 17 months of decomposition in the field (*Chapter 4*).

The objective of the research presented in Chapter 2 was to determine whether differences in the dominant vegetation type, brought about by changes in land-use and

plant species invasion, affected the magnitude of ecosystem C and N cycling. Since soil microbes are the dominant drivers of organic matter turnover and soil nutrient availability, and are regulated by the availability of labile C from plant litter inputs, we determined the quantity and quality of plant detrital inputs to soils among vegetation types. In some semiarid ecosystems, disturbance and species invasion may lead to ecosystem C and N loss and ecosystem degradation (Schlesinger et al. 1990). We used natural abundance $\delta^{15}N$ signatures of ecosystem pools to determine whether changes in vegetation type affected the ecosystem N balance.

The objective of Chapter 3 was to determine whether the timing of plant detrital inputs among distinct plant life-forms was responsible for the previously observed accumulation of NO_3^- in surface soils. Soil NO_3^- accumulation is thought to result from a C limitation to microbial growth. We stimulated soil C availability by releasing plant biomass *in situ* to the soil detrital pool three weeks prior to the summer dry season. We compared soil C availability and gross N cycling rates among treated and untreated soils of annual and perennial vegetation types on three occasions from late spring to late summer. We hypothesized that greater C availability, resulting in increased microbial biomass and C mineralization rates, would translate to greater N immobilization rates, and this would inhibit the accumulation of inorganic N in surface soils during the summer.

The objectives of Chapter 4 were to quantify the importance of current year plant detritus versus older soil organic matter as sources of substrates for microbial growth, and to examine whether differential substrate use affected the balance between microbial N mineralization and N immobilization processes. We labeled annual grass biomass with

^{13}C *in situ*, and tracked the fate and turnover of ^{13}C in labile organic matter pools over 17 months. We hypothesized that microbial utilization of recent substrates would increase from summer to autumn, and that microbial utilization of these substrates, with wider C:N ratios, would be associated with greater N immobilization rates.

The results of these studies should clarify the extent to which differences in plant life-form and phenology affect rates of organic matter input to soil, and identify some potential mechanisms that control plant-soil-microbe feedbacks over longer time-scales in semiarid ecosystems.

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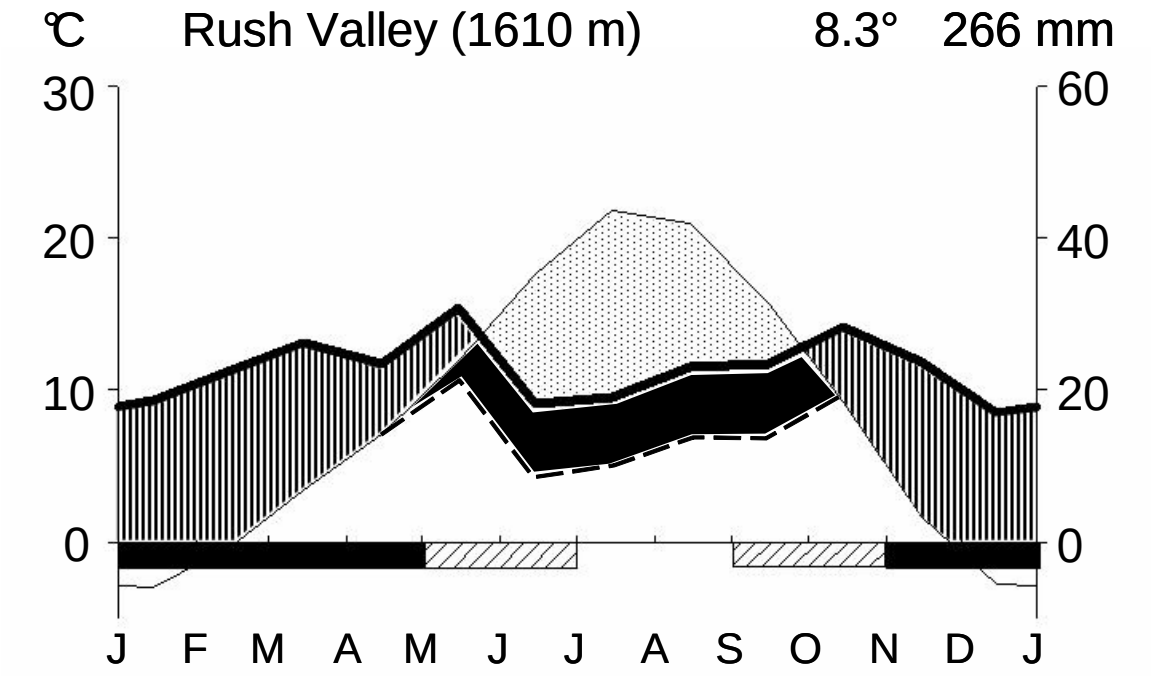

Figure 1-1. Ecological climate diagram for Rush Valley, UT. The thin line represents mean monthly temperature. The thick solid line represents mean monthly precipitation, and the dashed line represents mean monthly precipitation scaled to 10 ˚C = 30 mm precipitation. When drawn at these scales, the temperature curve approximates a potential evapotranspiration curve (format according to Walter 1979). Areas filled with vertical lines represent time-periods of relatively humid conditions, while horizontal dashes and dots represent dry and drought conditions, respectively. Solid bars at bottom of figure indicate months with mean daily minimum temperatures < 0 ˚C, and bars with diagonal shading indicate months with absolute minimum temperatures < 0 ˚C.

CHAPTER 2

DISTRIBUTION OF ECOSYSTEM C AND N WITHIN CONTRASTING VEGETATION TYPES IN A SEMIARID RANGELAND IN THE GREAT BASIN, USA[1]

Abstract: Semiarid sagebrush ecosystems are being transformed by wildfire, rangeland improvement techniques, and exotic plant invasions, but the effects on ecosystem C and N dynamics are poorly understood. We compared ecosystem C and N pools to 1-m depth among historically grazed Wyoming big sagebrush, introduced perennial crested wheatgrass, and invasive annual cheatgrass communities, to examine whether the quantity and quality of plant inputs to soil differs among vegetation types. Natural abundance $\delta^{15}N$ isotope ratios were used to examine differences in ecosystem N balance. Sagebrush-dominated sites had greater C and N storage in plant biomass compared to perennial or annual grass systems, but this was predominantly due to woody biomass accumulation. Plant C and N inputs to soil were greatest for cheatgrass compared to sagebrush and crested wheatgrass systems, largely because of slower root turnover in perennial plants. The organic matter quality of roots and leaf litter (as C:N ratios) was similar among vegetation types, but lignin:N ratios were greater for sagebrush than grasses. While cheatgrass invasion has been predicted to result in net C loss and ecosystem degradation, we observed that surface soil organic C and N pools were greater in cheatgrass and crested wheatgrass than sagebrush-dominated sites. Greater biomass

[1] Coauthors: John M. Stark, Urszula Norton, A. Joshua Leffler, Michael Peek, and Ron Ryel. With kind permission from Springer Media: Hooker, T. D., J. M. Stark, U. Norton, A. J. Leffler, M. Peek, and R. Ryel. 2008. Distribution of ecosystem C and N within contrasting vegetation types in a semiarid rangeland in the Great Basin, USA. Biogeochemistry 90:291-308.

turnover in cheatgrass and crested wheatgrass versus sagebrush stands may result in faster rates of soil C and N cycling, with redistribution of actively cycled N towards the soil surface. Plant biomass and surface soil $\delta^{15}N$ ratios were enriched in cheatgrass and crested wheatgrass relative to sagebrush-dominated sites. Source pools of plant available N could become ^{15}N enriched if faster soil N cycling rates lead to greater N trace gas losses. In the absence of wildfire, if cheatgrass invasion does lead to degradation of ecosystem function, this may be due to faster nutrient cycling and greater nutrient losses, rather than reduced organic matter inputs.

INTRODUCTION

Sagebrush-dominated ecosystems comprise extensive land areas in the Great Basin and intermountain regions of the western U.S. These ecosystems are being altered by grazing, rangeland improvement techniques, exotic plant invasions, and altered wildfire regimes. These disturbances affect the composition and structure of native vegetation, typically by causing a shift in dominance from shrubs to introduced perennial or invasive annual grasses (Stewart and Hull 1949, D'Antonio and Vitousek 1992, West 1999). Differences in the distribution and turnover of biomass among plant life-forms, and the degree of internal vs. external nutrient cycling in the plant-soil system are likely to play an important role in both short- and long-term ecosystem C and N storage and dynamics (Chapin et al. 1997). Given the large spatial extent of sagebrush ecosystems in the U.S. (over 60 million hectares, West and Young 2000), even small changes in rates of biogeochemical cycling due to vegetation change may have large ramifications for regional and global C and N budgets. However, in spite of the extensive land area

covered by sagebrush, surprisingly few data are available in the literature on ecosystem C and N pools and turnover rates in sagebrush-dominated systems.

Biogeochemical cycles in semiarid ecosystems are constrained by temporal and spatial variability (Burke 1989). Cold temperatures during the winter and low soil moisture in summer restrict the time frame for active plant growth and microbial activity to short periods in late spring and early autumn. When environmental conditions are adequate, rates of plant growth may be limited by soil N availability (James and Jurinak 1978, Bilbrough and Caldwell 1997, Duke and Caldwell 2001). Spatial patterns of plant cover and the life-form of vegetation types regulate soil organic matter accumulation and nutrient cycling rates (Charley and West 1977, Burke 1989, Vinton and Burke 1995, Schlesinger and Pilmanis 1998). The quantity and quality of plant organic matter inputs to soil via leaf litterfall and root turnover are key linkages driving soil microbial decomposition and plant nutrient availability. Increased C inputs, through differences in foliage and root turnover among different vegetation types (Caldwell et al. 1977, Gill and Jackson 2000, Belnap and Phillips 2001, Schenk and Jackson 2002), may increase N demand by soil microbes and reduce N available for plant uptake (Schlesinger and Peterjohn 1991, Hart et al. 1994). In contrast, increased quality of plant detrital inputs (i.e. lower litter C:N ratios) may increase N availability to plants via decreased microbial demand for inorganic N (Chen and Stark 2000, Carrera et al. 2003). What is not yet clear, is to what extent current shifts in dominant vegetation over large areas of the Great Basin and intermountain regions affect plant organic matter inputs, rates of soil organic matter turnover, and ecosystem C and N sequestration.

Shifts in vegetation type may alter the quantity and quality of organic matter

inputs to soil through differences in biomass allocation and the magnitude of plant internal nutrient cycling. In semiarid systems, shrubs (such as sagebrush) appear to have more extensive root systems than annual or perennial grasses (Schenk and Jackson 2002), such that changes in dominant vegetation type may alter the depth distribution of organic matter and nutrients (Jackson et al. 2000, Jobbagy and Jackson 2000) and rates of soil nutrient cycling. For example, Vinton and Burke (1995) found that differences in quantity, quality, and biomass distribution (root:shoot ratio) of shortgrass steppe vegetation affected soil potential C mineralization rates. Carrera et al. (2003) reported that in the Patagonian Monte, perennial grass-dominated sites had greater plant internal N cycling (leaf N resorption), higher leaf litter C:N, and lower soil potential N mineralization rates compared to sites dominated by evergreen shrubs. Similarly, Evans et al. (2001) found that cheatgrass invasion of Colorado Plateau grasslands increased the size and C:N ratio of surface litter pools compared to uninvaded grasslands, and reduced potential N mineralization rates.

The larger-scale consequences of vegetation change may include direct losses of C and N from long-lived woody tissues as a result of wildfire (Bradley et al. 2006), and reduced ecosystem productivity of introduced grasses compared to intact sagebrush ecosystems (Schlesinger et al. 1990, Ivans 2005, Prater et al. 2006); but the magnitude of such effects are unclear (see Huenneke et al. 2002). Land degradation following cheatgrass invasion and dominance, or conversion of sagebrush to perennial forage grasses, might also accelerate ecosystem N losses over inputs, resulting in enriched natural abundance $\delta^{15}N$ signatures (Evans and Ehleringer 1993, Hogberg 1997, Evans and Belnap 1999).

In this study we compare ecosystem C and N contents (above- and belowground biomass, surface litter, and soil organic matter pools to 1-m depth) and the quantity and quality of plant organic matter inputs in a native sagebrush ecosystem with two vegetation types that represent the most common alternative stable states following disturbance (cheatgrass and crested wheatgrass dominated ecosystems) in Great Basin rangelands. We hypothesized that differences in plant life-form strongly affect plant biomass distribution and the magnitude of plant internal vs. external nutrient cycling. Thus, the quality of plant organic matter inputs to soil would decrease, and litter quantity would increase in the order: cheatgrass, crested wheatgrass, and sagebrush. Consequently, we anticipated that plant biomass inputs would be lower in annual grass compared to native sagebrush ecosystems, leading to C and N losses from soil organic matter pools.

MATERIALS AND METHODS

Study site

This study was carried out on a Great Basin sagebrush rangeland in Rush Valley (Tooele County), Utah (112° 28’ W, 40° 17’ N, elevation 1610 m). The site has extensive, nearly monodominant stands of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young), crested wheatgrass (*Agropyron desertorum* (Fisch. ex. Link), var. ‘Nordan’), and cheatgrass (*Bromus tectorum* L.), and has been moderately grazed for over one hundred years (D. Johnson *personal communication*). Mean annual precipitation and temperature measured on-site over a 5-y period (1999-

2003) were 266 mm and 8.3ºC, respectively, which is similar to nearby long-term climate records (Vernon, UT, 21.5 km from research site, 273.1 mm and 8.7˚C, 1971-2000 means). Precipitation is distributed nearly evenly over the year, but soil water accumulation is restricted to the cooler autumn and winter months (November through March). Soils are derived from lacustrine (former Lake Bonneville) and alluvial sediments of primarily limestone deposits, have no root-restricting layer, and are classified as Erda silt loam, very deep, well drained, mixed, superactive, mesic Aridic Calcixerolls (A. Mitchell *personal communication*). Soils are non-saline within the surface 100 cm (EC < 2.0 dS m^{-1})(Table 2-1). Soil carbonates are mainly disseminated, with concentrations increasing from 10 to >25 g CO_3-C kg^{-1} soil with depth, and account for the majority (>70%) of total soil C to 100-cm depth.

Stands of both crested wheatgrass and cheatgrass vegetation were established in 1992 on areas formerly dominated by sagebrush. Crested wheatgrass was established to improve rangeland quality by disking to remove shrubs and then drill-seeding (30-cm row spacing). Cheatgrass established naturally with the onset of autumn rains after a summer wildfire consumed several large areas of sagebrush. Due to the long history of cheatgrass within the Great Basin (Pickford 1932, Mack 1981), it is likely that cheatgrass was already present in at least small amounts within the sagebrush stand at the time of disturbance.

In late 1998, four 22 x 22 m permanent plots were created in each vegetation type. Permanent plots were randomly located along two north-south and two east-west transects that crossed all three vegetation types. Transects were separated by at least 75 m, and plots of adjacent vegetation types within a transect were separated by

approximately 40 m. All measurements were made from random locations within each of the permanent plots. Field sampling included measurement of aboveground biomass, surface litter, plant root biomass, and soil to a 1-m depth. Due to the large spatial heterogeneity in plant cover in Great Basin sagebrush communities, surface litter, belowground biomass and soil organic matter pools within sagebrush plots were sampled in randomly selected paired locations beneath shrub canopies and in the shrub-interspace (within 1 m of the canopy sampling point). The areal extents of shrub-canopy and shrub-interspace microsites (average 38% and 62%, respectively), determined by the line-intercept method, were used to scale results to an areal basis.

Aboveground biomass and surface litter

Crested wheatgrass and cheatgrass vegetation was sampled by harvesting live and dead biomass bi-weekly during the growing season (less frequently in summer and autumn) in 2001 and 2002. Biomass was harvested from five randomly located quadrats per plot on each sampling date; crested wheatgrass quadrats were 25 x 25 cm, and cheatgrass quadrats were 10 x 10 cm. Plant samples were dried and prepared for elemental and isotopic analysis as described below. Peak aboveground biomass was used as an estimate of aboveground production in perennial and annual grass vegetation types. Aboveground production was estimated from the seasonal peak since the growing season is short for the annual grass, and growth is monotonic for the perennial grass in this semiarid ecosystem (see Sala and Austin 2000). Grazing management practices commonly include introducing cattle in mid- to late-summer; however, we excluded grazing from the site during the year that measurements were made to allow estimation of

above-ground plant biomass production and to reduce grazing-induced variability in soil characteristics. Our estimates of aboveground biomass production assume that herbivory by other animals (antelope, rabbits, and Mormon crickets) was negligible.

Total aboveground biomass of sagebrush vegetation was calculated from allometric equations (Rittenhouse and Sneva 1977, Uresk et al. 1977, Fransden 1983, Reiner 2004) based on measurements of each shrub >15 cm tall in the four 22 x 22 m permanent plots (n = 2660 plants). The average of values from all four allometric equations was used to estimate sagebrush aboveground biomass, as this average was closely correlated with biomass measured directly from destructive harvest of eight sagebrush spanning a wide range of plant sizes (90 to 4000 g/plant; $r^2 = 0.93$, slope = 0.95). Sagebrush aboveground biomass calculated in permanent plots ranged from 40 to 7500 g/plant. The aboveground biomass of destructively harvested shrubs was separated into foliage plus four classes of woody tissue: small, medium, and large branches (< 1.5, 1.5-3.0, and 3.0-4.0 cm circumference, respectively), and trunk (> 4.0 cm). Harvested materials were dried and ground for elemental and isotopic analysis. The proportion of biomass in each size-class was found to be logarithmically related to total shrub mass (g):

% small	= -0.043 ln(shrub mass) + 0.533	$r^2 = 0.68$
% medium	= -0.014 ln(shrub mass) + 0.253	$r^2 = 0.49$
% large	= 0.036 ln(shrub mass) - 0.122	$r^2 = 0.55$
% trunk	= 0.042 ln(shrub mass) + 0.141	$r^2 = 0.56$
% foliage	= -0.020 ln(shrub mass) + 0.207	$r^2 = 0.69$

These relationships were used to estimate the biomass of shrub components for each shrub measured in the four permanent plots. Aboveground biomass C and N contents

(Mg C ha^{-1} and kg N ha^{-1}) were estimated by multiplying C and N concentrations of biomass components by the mass of the component, and summed for each shrub. Natural abundance N isotope ratios ($\delta^{15}N$) were calculated by multiplying the δ-value of each biomass component by the component's relative contribution to shrub total N content. Senesced plant foliage and root biomass (from surface soils, see below) were analyzed for lignin concentration (ash-free) following forage fiber methodology (Goering and Van Soest 1970).

Surface litter C and N contents were determined for ten dates during the snow-free season from April 2001 to April 2002, and are presented as surface litter C and N content at the time of maximum plant aboveground biomass (late May for cheatgrass, mid-June for crested wheatgrass and sagebrush). Live and standing dead plant biomass was removed prior to collecting surface litter. Samples were brought back to the laboratory, dried (65˚C) and weighed, ground (60 mesh) with a Wiley mill, and subsampled for analyses of C and N concentration and isotope ratios.

Soil sampling

Soils were collected with a 5-cm diameter 'King-tube' (Giddings Machine Co., Windsor, CO), on 5 sampling dates (April 2001 to April 2002) from one randomly selected location in each of the four permanent plots of each vegetation type. Soil cores were separated into 0-10, 10-20, 20-40, 40-70, and 70-100 cm increments in the field, and stored in separate plastic bags on ice until returned to the laboratory. A second set of surface soil cores (0-10 and 10-20 cm) were collected within 30 cm of the first to provide sufficient soil for laboratory analyses.

Soils were sieved (<2 mm and <1 mm) to collect coarse fragments and roots the day following sampling. Roots were rinsed with deionized H_2O and dried, weighed and ground for elemental and isotopic analysis. Coarse fragments were dried and weighed to calculate fine soil bulk density (assuming particle density of 2.65 Mg m^{-3}). Soil moisture content was determined by mass-loss after drying for 48 hours at 105°C. A subsample of fine soil was dried and ground for determination of C and N concentrations and isotope ratios.

Soil organic C was determined following removal of carbonates by the acid fumigation procedure of Harris et al. (2001). Soil N concentrations and natural abundance $\delta^{15}N$ isotope ratios were determined using non-acid fumigated soil samples. Soil inorganic C was calculated as the difference in C from unfumigated (total C) and HCl-fumigated (organic C) samples. Total root biomass and soil C and N contents to 1-m soil depth were calculated by scaling pools to a mass per hectare basis for each depth, and summed for each plot; data presented are the average from five sampling dates. Total soil and root isotope ratios were calculated similarly, but values are weighted averages (based on C or N content) for each plot. All plant, litter, and soil C and N concentrations and isotope ratios were determined by continuous-flow direct combustion and mass spectrometry using a Europa 20/20 Mass Spectrometer (Europa Scientific, Crewe U.K.). Analytical precision was approximately 0.15 ‰ $\delta^{15}N$ over all sample analyses, with duplicate analysis of 10% of samples.

Soil NH_4^+ and NO_3^- concentrations were measured in 2M KCl extracts (1:10 soil:solution ratio), obtained in the field within 1 h of sample collection, and analyzed colorimetrically with a Lachat AE flow-injection Autoanalyzer (Lachat Instruments,

Milwaukee, WI, USA). Microbial biomass C and N were determined on sieved, field-moist soils by the chloroform fumigation-extraction method following Haubensak et al. (2002), using k_{EC} of 0.35 (Voroney et al. 1991) and k_{EN} of 0.54 (Brookes et al. 1985). Paired fumigated and non-fumigated soil samples were extracted with 0.5M K_2SO_4 (1:10 soil:solution ratio). Extracts were analyzed for organic C concentration with Phoenix 8000 TOC analyzer (Teledyne-Tekmar, Mason, OH, USA), and total soluble N (Lachat AE) following persulfate oxidation (Cabrera and Beare 1993).

Calculation of above- and belowground plant C and N inputs to soil

Aboveground plant C inputs to soil were assumed to equal maximum plant biomass for crested wheatgrass and cheatgrass vegetation. Sagebrush foliage C inputs to soil were assumed to equal foliage biomass C calculated from allometric equations described above, based on complete turnover of both ephemeral and over-wintering foliage on an annual basis (Evans and Black 1993, Welch 2005). Aboveground C inputs may be slightly overestimated if photodegradation results in significant mineralization of C from standing dead biomass and surface litter (Austin and Vivanco 2006, Brandt et al. 2007, Henry et al. 2008). No estimates of sagebrush woody litter inputs were made, since these inputs have very high spatial and temporal variability (West 1985) and contribute < 8% to annual litterfall (Mack 1977).

Annual aboveground plant N inputs to soil were calculated as:

$$\text{N input} = (1 - \text{NRE}) \cdot f_N \quad (1)$$

where NRE equals foliage N resorption efficiency, and f_N is foliage N content at peak biomass. Leaf N resorption efficiency was calculated directly based on differences in

leaf N concentration at maximum plant biomass and in early autumn following leaf senescence (prior to autumn rainfall). The decline in cheatgrass foliage N concentration after maximum biomass was assumed to represent N translocated to maturing seeds. Cheatgrass aboveground N inputs were calculated with and without accounting for N translocated to seeds, but statistical analysis was restricted to the conservative estimate of leaf N input (after translocation), since cheatgrass seeds may reside in soil for several years before germinating or being decomposed (Hulbert 1955, Billings 1994), and cheatgrass soil detrital pools may not be at steady-state. Belowground C and N inputs were calculated as the product of mean root C and N pool size (five sampling dates) and root turnover rate. Belowground biomass turnover was assumed to equal 1.0 yr^{-1} for cheatgrass, 0.5 yr^{-1} for crested wheatgrass (Gill and Jackson 2000), and 0.3 yr^{-1} for sagebrush (Caldwell et al. 1977). We assumed that there was no resorption of N from roots during senescence.

Statistical analysis

We used repeated measures analysis to evaluate the depth-distribution of soil C and N pools and isotope ratios, among vegetation types using PROC MIXED (SAS version 9.0, Cary NC). Vegetation type and sample depth were fixed effects, plots were random, with plot x vegetation type as the subject of repeated measure. We used information criteria (AICC and BIC) from several covariance structures to obtain the best model for each variable. Most variables conformed to split-plot residual design with regard to covariance of the error matrix. Variables were transformed when necessary to comply with model assumptions; data were most commonly natural log transformed.

The SLICE command was used to evaluate significant differences among vegetation types for each soil depth, and when significant, pairwise differences were used to compare each vegetation type at a specific soil depth. Analysis of variance was used to determine whether vegetation types differed for total ecosystem pools. Statistical differences were considered significant for $\alpha = 0.05$.

RESULTS

Distribution of Ecosystem C and N

Total ecosystem C content averaged 258 ± 11 Mg C ha^{-1} (mean ± 1 S.E.) to a 1-m depth across vegetation types, and was dominated by soil inorganic C pools. Organic C accounted for 29% of total ecosystem C storage, with no significant differences among vegetation types ($p=0.21$). Similarly, total ecosystem N content did not differ significantly among vegetation types ($p=0.17$), averaging 7936 ± 409 kg N ha^{-1}.

Aboveground biomass C pools in sagebrush were roughly three times those in cheatgrass or crested wheatgrass vegetation types, while N pools were only 36% greater in sagebrush compared to the grasses (Tables 2-2 and 2-3). Sagebrush foliage accounted for nearly half of aboveground N, but only 16% of aboveground C. The remaining N and C was found in live and standing dead woody biomass. Peak aboveground biomass C and N contents in cheatgrass and crested wheatgrass vegetation types were greater than sagebrush foliage ($p<0.002$ and $p<0.03$ for C and N contents, respectively). Aboveground biomass C:N ratios were highest for sagebrush woody biomass (89.2), while C:N ratios of live and senesced foliage did not differ significantly among

vegetation types (Table 2-4). Lignin concentrations and lignin:N ratios in sagebrush foliage were nearly three times those in cheatgrass or crested wheatgrass foliage ($p<0.001$).

Surface litter C and N pools in cheatgrass-dominated sites were significantly larger than in crested wheatgrass, while sagebrush surface litter was intermediate ($p<0.02$ and $p<0.01$, for C and N respectively; Tables 2-2 and 2-3). Spatial heterogeneity of surface litter C and N was large in sagebrush dominated sites. Litter pools beneath shrub-canopies (1.1 Mg C ha^{-1} and 61.6 kg N ha^{-1}, respectively) were approximately ten times those of shrub-interspaces (0.1 Mg C ha^{-1}, and 6.2 kg N ha^{-1}). Surface litter C:N ratios did not differ significantly among vegetation types.

Total root C and N pools to 1-m depth did not differ significantly among vegetation types, but the distribution of root C and N with soil depth varied among vegetation types (vegetation type x soil depth interaction $p<0.0001$)(Tables 2-2 and 2-3). More than 60% of total root C was found within the surface 0-20 cm soil beneath cheatgrass vegetation, compared to 51% in sagebrush and 38% in crested wheatgrass vegetation types. In the subsoil, cheatgrass root C was less than half that of crested wheatgrass and sagebrush vegetation types (Table 2-2). Root C:N ratios were not significantly different among vegetation types within the surface soil (0-10 cm, $p<0.05$)(Table 2-4), but C:N ratios of perennial plant roots doubled (>50:1) with increasing soil depth, and were significantly greater than cheatgrass roots between 10 and 40 cm (data not shown). Root lignin concentrations and lignin:N ratios in surface soil (0-10 cm) were significantly higher in sagebrush roots compared to crested wheatgrass, while cheatgrass was intermediate ($p<0.01$ for lignin and lignin:N ratios; Table 2-4).

We found no significant differences in total soil C or N pools among vegetation types within 1-m depth. In addition, the distribution of soil bulk density (Table 2-1), coarse fragment content, and inorganic C with depth did not differ significantly among vegetation types. Coarse fragments (>2 mm) accounted for only 1.1% of soil mass in surface (0-10 cm) soil and 4.5% in subsoil (70-100 cm), averaging 2.4 ± 1.1% across all soil samples collected. However, surface soils (0-10 cm) of cheatgrass dominated sites had significantly larger organic C ($p<0.019$) and N ($p<0.012$) pools compared to sagebrush soils, and crested wheatgrass soil C and N pools were intermediate (Tables 2-2 and 2-3). Soil organic C:N was highest in the surface soil (approximately 10.7) and decreased with depth to approximately 7.8 at 70-100 cm.

Microbial biomass C and N content to 1 m accounted for approximately 2.8 % and 4.0 % of soil organic C and soil N pools, respectively, but did not differ significantly among vegetation types. Microbial C and N contents declined significantly with depth ($p<0.0001$ for both), with no significant difference among vegetation types (Tables 2-2 and 2-3). Inorganic N pools ($NH_4^+ + NO_3^-$) declined significantly with soil depth (Table 2-3). Averaged across all five sampling dates, NH_4^+ accounted for 48% of soil inorganic N in surface soil, and 27% in the subsoil. There was little difference in soil NH_4^+ pools among sampling date or among vegetation types ($p>0.2$), but NO_3^- increased during the summer dry-season (Figure 2-1), particularly in surface and subsurface soils beneath cheatgrass. Soil gravimetric water content, averaged across the five sampling dates, differed significantly with soil depth ($p<0.0001$) and among vegetation types ($p<0.003$)(data not shown). Soil water content was highest in cheatgrass and lowest in crested wheatgrass within the surface soil (0-10 cm) and subsoil (below 20 cm).

Estimates of Plant Above- and Belowground inputs to soil

Total plant detrital C inputs to soil were greatest in cheatgrass and crested wheatgrass compared to sagebrush vegetation types (0-10 cm: $p<0.02$, 0-100 cm: $p<0.01$, Table 2-5). Similarly, plant N inputs were significantly greater in cheatgrass vs. the other vegetation types, particularly for the surface soil (0-10 cm: $p<0.016$, 0-100 cm: $p<0.03$).

Natural abundance $\delta^{15}N$ stable isotope ratios

Cheatgrass aboveground biomass $\delta^{15}N$ (at peak biomass) was significantly enriched (6.6 ‰, $p<0.001$) relative to crested wheatgrass (5.2 ‰), and sagebrush whole plant biomass (2.9 ‰) and foliage (3.6 ‰, $p<0.001$; Figure 2-2). Across the growing season, $\delta^{15}N$ of cheatgrass foliage declined from 8.5 ‰ in spring to approximately 5.5 ‰ shortly after plant senescence, while crested wheatgrass and sagebrush foliage $\delta^{15}N$ ratios declined by 1.0 ‰ (data not shown). Surface litter pools were slightly enriched beneath cheatgrass compared to the other vegetation types (Figure 2-2), but this difference was not significant ($p=0.15$). Root biomass $\delta^{15}N$ signatures were also significantly higher in cheatgrass and crested wheatgrass versus sagebrush dominated soils overall ($p<0.014$). Differences in root $\delta^{15}N$ among vegetation types were greatest in surface soil (0-10 and 10-20 cm, $p<0.0001$ and $p<0.02$), where cheatgrass and crested wheatgrass roots were 1.1 to 2.9 ‰ enriched relative to sagebrush roots. Soil $\delta^{15}N$ isotope ratios were not significantly different among vegetation types overall ($p=0.11$), and were nearly constant with depth ($p=0.07$). However, in surface soil cheatgrass and crested wheatgrass soil $\delta^{15}N$ signatures were up to 1.1 ‰ enriched relative to sagebrush soils (Figure 2-2,

$p<0.03$). Root biomass $\delta^{15}N$ was significantly correlated ($r=0.77$, $p<0.001$) with surface soil $\delta^{15}N$ across vegetation types. Weighted average $\delta^{15}N$ of ecosystem N pools were slightly, but not significantly, enriched in cheatgrass and crested wheatgrass sites (9.0 ± 0.3 ‰) compared to sagebrush sites (8.5 ± 0.3 ‰).

DISCUSSION

Influence of vegetation type on the quantity and quality of plant organic matter inputs to soil

We found substantial differences in the quantity of plant organic matter inputs to soil among monodominant stands of sagebrush, crested wheatgrass, and cheatgrass vegetation types. Interestingly, the quantity of plant C inputs to soil (comparable to net primary production, NPP) was nearly twice as large in cheatgrass and crested wheatgrass systems as in sagebrush systems (Table 2-5). This pattern strongly contrasts with our initial hypothesis, that C inputs to soil would be lower in cheatgrass versus sagebrush dominated sites, and is driven by greater foliage and root turnover in annual and perennial grasses compared to sagebrush. Our results are similar to estimates of plant inputs derived from literature data (Table 2-6) and to NPP of sagebrush-steppe using eddy covariance methods in Idaho (Gilmanov et al. 2003). Between vegetation types, Huenneke et al. (2002) reported slightly greater aboveground NPP in grass versus shrub dominated areas in the Chihuahuan desert, and Stewart and Hull (1949) found comparable production between crested wheatgrass and cheatgrass in Idaho.

Plant N inputs to soil were more than twice as large in cheatgrass compared to perennial grass and sagebrush systems (Table 2-5). The greater N inputs in cheatgrass-

dominated soils was largely due to greater root N turnover (45 vs. 13 kg N ha^{-1} yr^{-1}), since foliar N resorption efficiencies (Table 2-5) and plant biomass C:N ratios (Table 2-4) were similar among vegetation types. This is consistent with greater biomass turnover and more 'open' nutrient cycling in annual grass versus perennial plant dominated ecosystems (Jones and Woodmansee 1979), and may explain the faster soil N cycling rates in cheatgrass versus sagebrush reported by others (Booth et al. 2003, Saetre and Stark 2005). Other studies have reported foliar N loss in annual grasses during the growing season (Woodmansee and Duncan 1980, Evans et al. 2001, Svejcar and Sheley 2001, Eviner 2004); we interpret this as primarily translocation of N to maturing seeds. Volatile N losses are unlikely to explain the seasonal decline in cheatgrass foliar N. Cheatgrass foliar $\delta^{15}N$ declined by approximately 3 ‰ during the growing season, but NH_3 volatilization should result in leaf $\delta^{15}N$ enrichment (Hogberg 1997).

The similarity in the quality (as C:N ratio) of both live and senesced plant foliage and roots among vegetation types is surprising compared to work from other semiarid ecosystems (Vinton and Burke 1995, Evans et al. 2001, Carrera et al. 2003) and given the large differences in plant functional type in this study. However, sagebrush foliage and fine roots had greater lignin concentrations and lignin:N compared to cheatgrass or crested wheatgrass (Table 2-4), which could affect accumulation of surface litter. Woody litter inputs beneath sagebrush canopies, although not evaluated in terms of plant inputs in this study, might be expected to increase surface litter accumulation compared to grass dominated sites. Instead, both surface litter pools and aboveground inputs in sagebrush sites were one-half those in cheatgrass stands, suggesting that neither higher lignin concentrations or woody litter inputs had much effect on surface litter turnover and

accumulation in this ecosystem.

Greater C and N inputs in grass- versus sagebrush-dominated ecosystems may be responsible for the larger surface soil C and N pools observed in this study (Tables 2-2 and 2-3). Alternatively, larger surface soil N pools could be due to greater N_2-fixation by cryptobiotic crusts; however, if this were the case then natural abundance ^{15}N isotope ratios would be expected to be less enriched (closer to 0 ‰) in surface soils with greater N content (Evans and Ehleringer 1993). Instead, cheatgrass and crested wheatgrass soils had more enriched $\delta^{15}N$ signatures than sagebrush soils (Figure 2-2). This is similar to results of Booth et al. (2003) and suggests greater losses of ^{15}N depleted N-forms (Hogberg 1997, Amundson et al. 2003). Given our results, the ecosystem-level response to vegetation change may be more complicated than simply greater retention of actively cycled N or increased trace gas N loss.

Differences in the quantity of plant inputs to soil among vegetation types may also affect the retention and cycling of organic matter within deeper soil layers. Our calculations of subsoil C inputs suggest greater inputs in crested wheatgrass sites compared to sagebrush or cheatgrass dominated sites (indicated by the difference between C inputs in 0-10 and 0-100 cm increments in Table 2-5). Smaller subsoil C inputs were due to small root biomass pools in cheatgrass, and both small root biomass and slow root turnover estimates in sagebrush soils. Over time, ecosystem C storage could increase in crested wheatgrass compared to sagebrush sites, since decomposition rates are slower at depth, and a greater proportion of recalcitrant C remains compared to surface soils (Gill and Burke 2002).

We observed accumulation of soil NO_3^- during the summer in all vegetation types

(Figure 2-1), but the largest pools were found in cheatgrass surface and subsurface soils. This appears to be a general phenomenon in semiarid ecosystems (Jones and Woodmansee 1979, Jackson et al. 1988, Davidson et al. 1990, Svejcar and Sheley 2001, Booth et al. 2003, Sperry et al. 2006). Soil NO_3^- accumulation may be a consequence of enhanced microbial activity after infrequent summer precipitation events (Cui and Caldwell 1997, Austin et al. 2004) and lower rates of inorganic N consumption as soils dry (Low et al. 1997), while greater NO_3^- accumulation in surface soils beneath cheatgrass versus perennial vegetation could be due to the lack of plant N uptake after annual grass senescence. The mechanisms resulting in greater subsoil NO_3^- beneath cheatgrass are not clear, but could result from: 1) leaching of NO_3^- from surface soils during cold-season soil water recharge, or 2) *in situ* net nitrification in deeper soil horizons due to microbial C limitations. Unfortunately, the relative importance of these mechanisms has not been determined. In any case, leaching of elevated NO_3^- pools below the shallow rooting zone during soil water recharge may be an important mechanism for ecosystem N loss from cheatgrass stands over time. Results from other work reveal a large potential for NO_3^- accumulation below the rooting zone in arid and semiarid systems (Walvoord et al. 2003, Jackson et al. 2004).

Integrating the N cycle with ecosystem $\delta^{15}N$

Ecosystem N pools in this study exhibit enriched $\delta^{15}N$ signatures (9.0 ‰) compared to other temperate ecosystems (Martinelli et al. 1999), which may be a consequence of semiarid climate, historical land use, or soils derived from lacustrine sediments. Amundson et al. (2003) and Austin and Vitousek (1998) suggest that drier

climates display enriched $\delta^{15}N$ signatures because ^{15}N-depleted gaseous losses (e.g. NH_3 volatilization, and NO and N_2O emissions) exceed leaching losses (Peterjohn and Schlesinger 1990). A history of grazing may also be a factor (Sparks et al. 1990, West 1999), with loss of cryptobiotic crust communities after disturbance (Skujiņš and West 1974, West and Skujiņš 1977) resulting in enriched $\delta^{15}N$ signatures of plant available N over time (Evans and Belnap 1999). Lacustrine sediments are a common soil parent material in the Great Basin and may contain older ^{15}N-enriched organic matter. This might explain the lack of a pattern in soil $\delta^{15}N$ with depth (Figure 2-2), in contrast to nutrient poor aeolian-derived soils of the Colorado plateau that display strong ^{15}N enrichment with depth (see Evans and Ehleringer 1993, Sperry et al. 2006).

The differences in plant $\delta^{15}N$ among vegetation types observed in this study are unlikely to be due to differences in plant physiological isotopic fractionation during N assimilation. While plants may fractionate against ^{15}N when plant N assimilation rather than soil N availability is the rate limiting step (Mariotti et al. 1982, Evans 2001), inorganic N pools during periods of active growth were smaller than concentrations where physiological fractionation is expected to be significant (Kolb and Evans 2003). Differences in plant uptake of NH_4^+ vs. NO_3^- are also unlikely to explain the observed patterns. Cheatgrass soils have the largest NO_3^- pools when germination begins in autumn (Figure 2-1, see also Booth et al. 2003). However, $\delta^{15}N$ of NO_3^- is depleted relative to NH_4^+ (Handley and Raven 1992), while cheatgrass foliage $\delta^{15}N$ signatures were significantly enriched compared to crested wheatgrass or sagebrush (Figure 2-2). Instead, differences in plant $\delta^{15}N$ signatures among vegetation types likely reflect differences in $\delta^{15}N$ of labile (plant available) N pools.

We propose two possible mechanisms that could result in ^{15}N enrichment of plant available N in grass- versus sagebrush-dominated ecosystems. The first mechanism involves NO_3^- accumulation during the dry-season and translocation of the more ^{15}N-depleted NO_3^- below the rooting zone during cold-season soil water recharge. Nitrification results in isotopically depleted NO_3^- but enriched NH_4^+ pools (Handley and Raven 1992). While the magnitude of NO_3^- movement into subsoils of Great Basin ecosystems remains unknown, work in other semiarid and arid systems suggests that NO_3^- transport below the rooting zone may be substantial (Walvoord et al. 2003, Jackson et al. 2004).

The second mechanism involves stimulation of soil C and N cycling rates in response to greater plant C and N inputs. Since nitrification consumes a substantial proportion of gross N mineralization in semiarid systems (Schimel et al. 1989, Davidson et al. 1990, Smart et al. 1999, Booth et al. 2003, Saetre and Stark 2005), accelerated N cycling rates could increase trace gas loss of ^{15}N-depleted NO and N_2O (from nitrification, nitrifier-denitrification, or denitrification processes; Firestone and Davidson 1989, Hogberg 1997, Smart et al. 1999, Stark et al. 2002), and result in isotopic enrichment of actively cycled N. This mechanism may also be consistent with observed shifts in the distribution of actively cycled organic matter towards the soil surface after vegetation change. Over longer time-scales, both mechanisms could lead to ecosystem degradation due to a reduction in the amount of actively cycled N.

Cheatgrass invasion has been shown to substantially increase wildfire frequency (Whisenant 1990, D'Antonio and Vitousek 1992, Brooks and Pyke 2001). The cheatgrass stands examined in this study did not burn during the 10 years since the initial cheatgrass

invasion, and thus our discussion has focused on differences in C and N cycling unrelated to repeated burning. Increased wildfire frequency could have important impacts on nutrient pools and cycling rates; however the magnitude of these effects will be highly dependent on the return interval and intensity of fires. Assuming that wildfires consume all senesced aboveground plant tissue and surface litter and that all of the N contained in these components is lost from the cheatgrass system, N loss from a single fire would be approximately 70 kg N ha^{-1}, or <1% of the total ecosystem N. The fire return interval would determine whether sufficient time occurred to allow replenishment of this N through wet and dry N deposition and biological N fixation. The long-term impact of indirect effects of fire (e.g. increased N mineralization rates) are even more difficult to predict since they can have both positive effects (e.g. increased plant production and N uptake; increased N-fixation) and negative effects (e.g. increased denitrification and gaseous N loss; erosion). Therefore, it is not clear how increased wildfire frequencies associated with cheatgrass will contribute to loss of nutrients and ecosystem degradation.

In conclusion, our results suggest that plant detrital inputs and cycling of labile C and N may be accelerated in disturbed ecosystems dominated by introduced grasses such as cheatgrass and crested wheatgrass compared to native sagebrush. If cheatgrass invasion and dominance does lead to degradation of ecosystem function, this may be due to faster nutrient cycling and greater losses, rather than reduced organic matter inputs. The increase in wildfire frequency and severity associated with the cheatgrass-wildfire cycle may in turn affect ecosystem C and N cycling through direct C and N losses, while accelerated rates of nutrient cycling may amplify already substantial trace gas emissions to the atmosphere from semiarid rangelands (Bowden 1986, Schlesinger et al. 1990).

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Table 2-1. Site characteristics, Rush Valley, Utah

Site characteristic	Cheatgrass	Crested Wheatgrass	Sagebrush Canopy	Sagebrush Interspace
Plant cover (%) [1]	80 %	37 %	15 %	<1 %
Root length density ($mm\ cm^{-2}$) [2]	9.1	4.0	1.4	n.d.
Average root diameter (mm) [2]	0.20	0.22 – 0.24	0.26 – 0.30	n.d.
Textural class	silt loam	silt loam	loam	silt loam
% clay	15.0%	14.5%	15.5%	14.0%
% silt	52.5%	53.0%	48.0%	48.0%
pH [3]	7.5	7.5	7.2	7.7
Total soluble P ($mg\ P\ kg^{-1}$ soil) [3]	0.25 ab	0.30 a	0.31 a	0.15 b
Electrical conductivity ($dS\ m^{-1}$) [3]	0.50 a	0.28 b	0.55 a	0.25 b
Fine soil bulk density ($Mg\ m^{-3}$) [4]				
0-10 cm	1.00	1.01	0.98	1.02
10-20 cm	1.13	1.16	1.12	1.20
20-40 cm	1.10	1.15	1.22	1.26
40-70 cm	1.18	1.31	1.25	1.25
70-100 cm	1.10	1.25	1.07	1.17

Sagebrush sites were stratified into areas beneath the outer extent of sagebrush canopies and interspace areas outside of sagebrush canopies. Canopy-affected areas represented 38% and interspace areas represented 62% of the total area of sagebrush ecosystems, based on line-intercept measurements.

1. Percentage of plot area covered by live leaf tissue at maximum biomass.

2. For the 0-10 cm soil depth, based on minirhizotron data.

3. Saturated paste extracts, 0-10 cm soil depth.

4. Coarse fragments (>2 mm) accounted for 1.1 to 4.5% of soil mass.

n.d. – No data.

Within a row, values followed by same letter are not significantly different ($p > 0.05$)

Table 2-2. Ecosystem C pools in three vegetation types in Rush Valley, Utah

Ecosystem Pool	Cheatgrass	Crested wheatgrass	Sagebrush			
			Areal average [1]	Beneath canopy	Interspace	Model SE [2]
	---------- Mg C ha^{-1} ----------					
Aboveground plant biomass C	1.2 (0.1) b	1.3 (0.1) b	3.8 (0.7) a			
Wood	n.a.	n.a.	3.2 (0.5)			
Foliage	1.2 (0.1) a	1.3 (0.1) a	0.6 (0.1) b			
Surface litter C	0.9 (0.1) a	0.4 (0.1) b	0.6 (0.1) ab			
Root C (0-100 cm)	2.0 (0.3)	3.1 (0.4)	2.4 (0.3)			
Soil organic C (0-100 cm)	72.1 (3.9)	69.1 (3.1)	62.0 (4.2)			
Root C	---------- kg C m^{-3} ----------					
0-10 cm	1.00	0.69	0.81	1.40	0.46	(0.22)
10-20 cm	0.26 b	0.48 a	0.42 a	0.48	0.36	(0.11)
20-40 cm	0.15 b	0.37 a	0.20 b	0.27	0.15	(0.07)
40-70 cm	0.09 b	0.26 a	0.18 a	0.15	0.20	(0.06)
70-100 cm	0.01 c	0.14 a	0.06 b	0.07	0.05	(0.02)
Soil organic C						
0-10 cm	15.92 a	14.28 ab	12.90 b	14.24	12.15	(2.84)
10-20 cm	10.51	10.99	9.59	9.75	9.47	(2.19)
20-40 cm	7.72	7.25	6.64	7.07	6.40	(1.52)
40-70 cm	6.08	5.93	5.01	5.43	4.76	(1.19)
70-100 cm	4.11	3.86	3.63	3.38	3.75	(0.79)

Table 2-2. (continued)

Ecosystem Pool	Cheatgrass	Crested wheatgrass	Sagebrush			
			Areal average [1]	Beneath canopy	Interspace	Model SE [2]
Microbial C	----------	----------	kg C m^{-3}	----------	----------	
0-10 cm	0.52	0.41	0.39	0.50	0.32	(0.18)
10-20 cm	0.31	0.24	0.27	0.35	0.22	(0.10)
20-40 cm	0.18	0.28	0.24	0.29	0.20	(0.08)
40-70 cm	0.14	0.15	0.14	0.18	0.12	(0.05)
70-100 cm	0.08	0.08	0.09	0.11	0.08	(0.03)

1. Weighted average of sagebrush canopy and interspace microsites, based on areal extent.

2. Back-transformed standard error for differences among vegetation types within a soil depth.

Within a row, means with the same lowercase letter are not significantly different ($p > 0.05$).

Table 2-3. Ecosystem N pools in three vegetation types in Rush Valley, Utah

Ecosystem Pool	Cheatgrass	Crested wheatgrass	Sagebrush			
			Areal average [1]	Beneath canopy	Interspace	Model SE [2]
	---------- kg N ha^{-1} ----------					
Aboveground plant biomass N	53.8 (5.9) b	48.1 (1.9) b	68.3 (11.5) a			
Wood	n.a.	n.a.	35.7 (11.5)			
Foliage	53.8 (5.9) a	48.1 (1.9) a	32.7 (5.7) b			
Surface litter N	43.4 (5.2) a	13.2 (3.2) b	27.1 (4.3) ab			
Root N (0-100 cm)	76.8 (14.1)	85.9 (12.2)	76.3 (8.1)			
Soil N (0-100 cm)	8072 (351)	7977 (354)	7255 (268)			
Root N (g N m^{-3})						
0-10 cm	44.6	25.4	41.1	74.8	20.2	(9.1)
10-20 cm	10.3	12.3	9.5	11.2	8.1	(3.1)
20-40 cm	4.4 b	7.7 a	3.7 b	4.8	3.1	(1.5)
40-70 cm	3.8	6.2	3.1	2.8	3.3	(1.3)
70-100 cm	0.5 c	4.8 a	1.8 b	1.8	1.8	(0.4)
Soil N (kg N m^{-3})						
0-10 cm	1.57 a	1.37 ab	1.21 b	1.25	1.18	(0.19)
10-20 cm	1.00	1.04	0.94	0.95	0.93	(0.15)
20-40 cm	0.80	0.85	0.82	0.89	0.79	(0.13)
40-70 cm	0.81	0.79	0.67	0.72	0.64	(0.11)
70-100 cm	0.54	0.50	0.43	0.42	0.48	(0.07)
Microbial N (g N m^{-3})						
0-10 cm	79.4	70.9	72.6	90.9	61.6	(10.6)
10-20 cm	61.3	53.1	45.7	52.4	41.3	(6.5)
20-40 cm	27.8	35.2	31.7	35.6	29.3	(3.7)
40-70 cm	19.3	28.5	22.4	20.6	23.9	(2.6)
70-100 cm	18.1	15.7	14.4	14.6	14.1	(1.7)

Table 2-3. (continued)

Ecosystem Pool	Cheatgrass	Crested wheatgrass	Sagebrush			Model SE [2]
			Areal average [1]	Beneath canopy	Interspace	
Soil NH_4^+ (g N m^{-3})						
0-10 cm	1.66	1.56	1.32	1.45	1.25	(0.20)
10-20 cm	0.86	0.97	1.24	1.27	1.24	(0.19)
20-40 cm	0.64	0.74	0.89	0.91	0.81	(0.08)
40-70 cm	0.45	0.56	0.62	0.61	0.64	(0.08)
70-100 cm	0.36	0.33	0.37	0.35	0.37	(0.04)
Soil NO_3^- (g N m^{-3})						
0-10 cm	3.70 a	2.61 ab	2.00 b	2.11	1.98	(0.22)
10-20 cm	2.13	2.00	1.67	1.77	1.62	(0.11)
20-40 cm	2.00	2.07	1.57	1.72	1.50	(0.13)
40-70 cm	2.12 a	1.25 b	1.07 b	1.18	1.01	(0.08)
70-100 cm	2.29 a	1.12 b	0.98 b	1.07	0.91	(0.12)

1. Weighted average of sagebrush canopy and interspace microsites based on the areal extent of the two microsites.
2. Back-transformed standard error for differences among vegetation types within a soil depth, from repeated measures ANOVA. Within a row, means with the same letter were not significantly different ($p > 0.05$).

Table 2-4. Characteristics of organic matter quality across vegetation types.

Ecosystem Pool	Cheatgrass	Crested wheatgrass	Sagebrush
Aboveground biomass C:N	22.9	26.9	55.7
Wood C:N			89.2
Live Foliage C:N	22.9	26.9	21.6
Senesced Foliage C:N	46.9	52.3	55.8
Foliar lignin (g/kg)	44.6 b	42.9 b	119.1 a
Foliage lignin:N	4.93 b	5.60 b	12.50 a
Surface litter C:N	21.2	29.7	21.3
Root biomass			
0-10 cm C:N	27.1	28.8	23.8
0-100 cm C:N	27.4 b	37.5 a	27.7 b
Root lignin (g/kg)	121.1 ab	90.07 b	164.8 a
Root lignin:N	7.30 ab	6.60 b	10.41 a
Soil organic matter C:N (0-10 cm)	10.4	10.6	10.7

Values are means from four field plots.
C:N ratio of live foliage represents values at peak plant biomass.
Lignin concentrations (ash-free) were measured on senesced foliage; root lignin concentrations were measured on a composite sample from the 0-10 cm soil depth over five sampling dates.
Within a row, values followed by same letter are not significantly different ($p > 0.05$).

Table 2-5. Estimates of aboveground and belowground plant C and N inputs to soil

	Cheatgrass	Crested wheatgrass	Sagebrush
Biomass turnover (AG / BG) † (yr^{-1})	1.0 / 1.0	1.0 / 0.50	1.0 / 0.30
	C inputs to soil (Mg C ha^{-1} yr^{-1})		
Aboveground inputs (AG)	1.23	1.29	0.62
Belowground inputs (BG)			
0-10 cm	1.08	0.34	0.25
0-100 cm	1.96	1.54	0.70
Total C inputs			
AG + 0-10 cm	2.31 a	1.63 ab	0.87 b
AG + 0-100 cm	3.19 a	2.83 a	1.32 b
N Resorption Efficiency ‡	0.54	0.58	0.56
	N inputs to soil (kg N ha^{-1} yr^{-1})		
Aboveground inputs (AG)	19.9	17.3	15.35
Belowground inputs (BG)			
0-10 cm	44.6	12.7	13.13
0-100 cm	76.8	43.0	22.88
Total N inputs			
AG + 0-10 cm	64.5 a	30.0 b	28.49 b
AG + 0-100 cm	96.7 a	60.3 ab	38.24 b

†Shows turnover rates assumed for calculations of inputs; aboveground input assumes that all leaf C is returned to soil surface annually; belowground turnover rates are based on literature estimates (see text).

‡ Foliar resorption efficiency estimated from leaf harvests. We assume no root N resorption during plant senescence.

Table 2-6. Carbon and nitrogen pools of semiarid ecosystems reported in the literature

Site	MAT/MAP (˚C / mm)	Soil depth sampled (cm)	Above-ground biomass †	Surface litter	Roots	Soil	Above-ground biomass †	Surface litter	Roots	Soil
Annual Grass			C pools (Mg C ha^{-1})				N pools (kg N ha^{-1})			
CA[1]	9 / 486	30	0.8-2.0	0.8-2.2	2.2-3.6		43-65	49	61	3185
CA[2]	16 / 300	100	2.7		4.5	92	100		220	8900
WA[3]	7 / 220	20	0.6-1.0	0.6-0.9			14-51	13-28		2200
WA[4]	8 / 250	30	0.25	0.35	0.64	17.7				
This study	8 / 240	100	1.2	0.9	2.0	72.1	54	43	77	8073
Perennial Grass										
WA[4]	8 / 250	30	0.34	0.3	0.99	15.2				
UT[5]	7 / 244	40	1.1	1.8	4.6		26	70	240	
ID[6]	8 / 300	90	0.7-1.4		5.3		44-67		53-80	
Arg.[7]	15 / 600	100	1.5	0.5	3.8		22	15	140	6400
This study	8 / 240	100	1.3	0.4	3.1	69.1	48	13.2	86	7977
Sagebrush										
CO[8]	7 / 270	45	2.7 [0.5]†	2.2	3.8	41.3	61 [16]†	43	61	5293
ID[9]	7 / 250		6.5		5.2					
UT[5,10]	7 / 244	90	3.0 [0.3]	4.5	4.2	52	57 [17]	35	157	5200
This study	8 / 240	100	3.8 [0.6]	0.5	2.4	62.0	68 [33]	27	76	7255

† - Numbers in brackets represent sagebrush foliage, if reported.

Superscript numbers refer to the following citations: (1) Jones and Woodmansee (1979) and Woodmansee and Duncan (1980), (2) Brenner et al. (2001); California chronosequence < 10,000 year old soils, (3) Rickard (1985); data reported as range of low and high elevation sites, (4) Svejvar and Sheley (2001), (5) Shinn et al. (1975); 6 grass and 6 shrub dominated sites in Curlew Valley, (6) Hull and Klomp (1975); crested wheatgrass biomass 5-10 years after sagebrush removal at high and low productivity sites (range), (7) Montani et al. (1996) and Brevedan et al. (1996); perennial grass in semiarid Argentina, (8) Redente et al. (1985), (9) Pearson (1965); Snake River sagebrush and *Stipa*, (10) West and Klemmedson (1978).

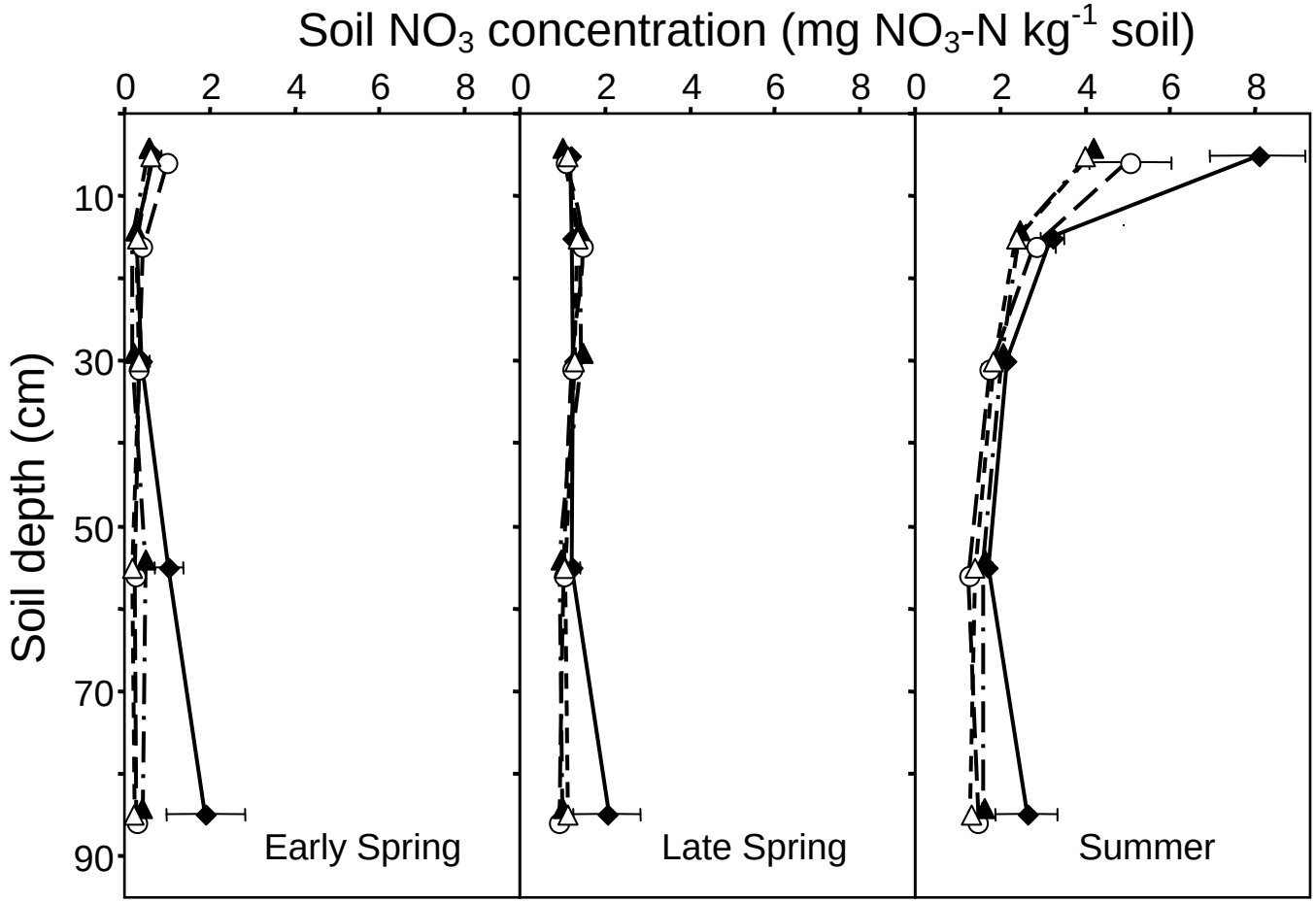

Figure 2-1. Seasonal changes in soil NO3- concentrations in three vegetation types. Symbols: cheatgrass (solid diamonds), crested wheatgrass (circles), sagebrush-canopy (solid triangles), sagebrush-interspace (hollow triangles). Error bars (±1 s.e.; n = 4).

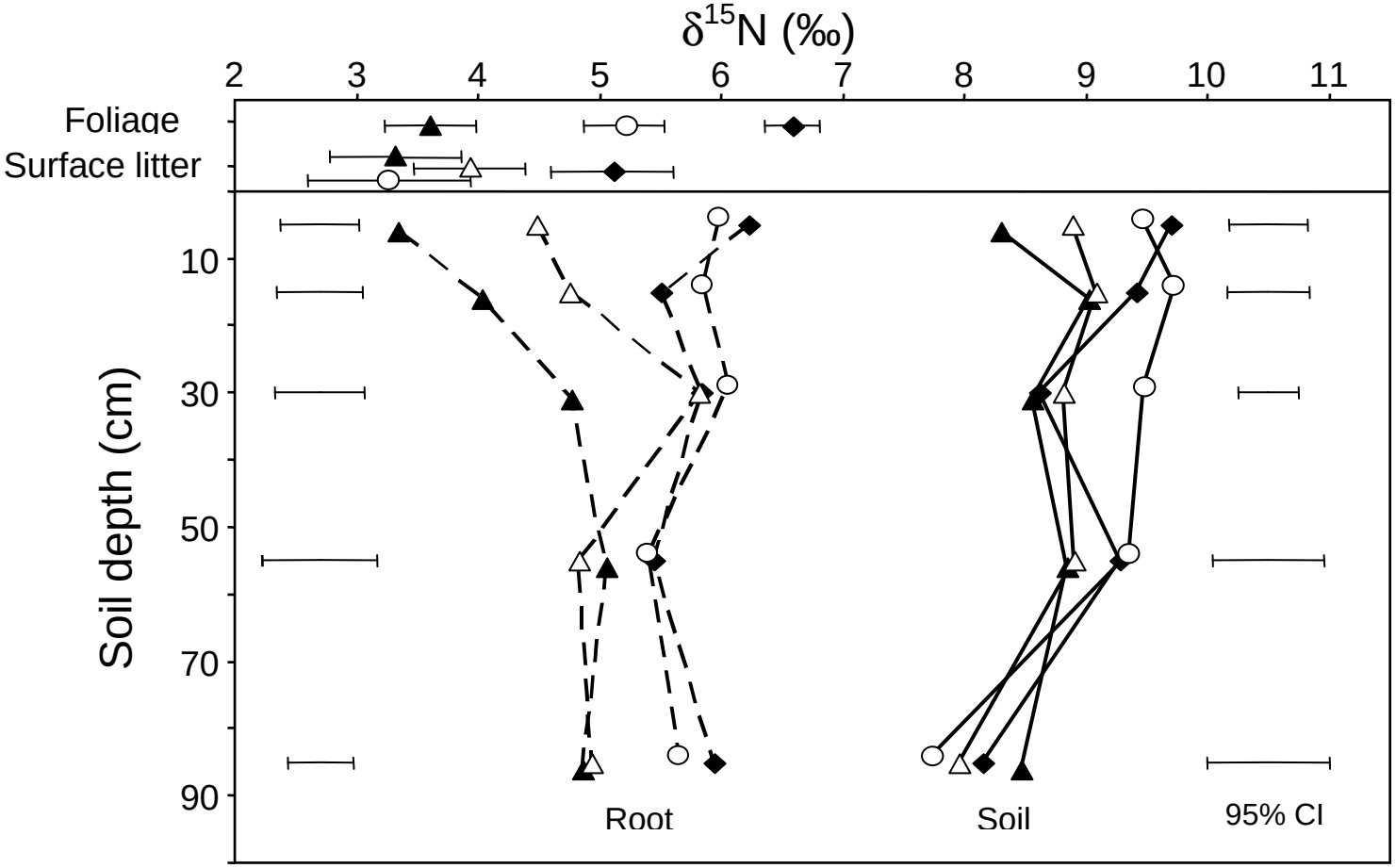

Figure 2-2. Natural abundance $\delta^{15}N$ for plant biomass, detritus and soil N pools. Symbols as in Figure 2-1. Symbols connected by dashed lines indicate root $\delta^{15}N$ ratios; solid lines indicate soil $\delta^{15}N$ ratios. Error bars represent 95% confidence intervals (n=4).

CHAPTER 3

SOIL C AND N CYCLING IN THREE SEMIARID VEGETATION TYPES: RESPONSE TO AN *IN SITU* PULSE OF PLANT DETRITUS[1]

Abstract: Plant detritus is an important source of labile C that drives soil microbial growth and regulates the balance of N mineralization and immobilization. In semiarid ecosystems, timing of plant detrital inputs may be especially important in regulating microbial C and N cycling because of the relatively short window of time when moisture is available. Low soil moisture in early summer may inhibit microbial colonization of recently released detritus, resulting in C-limitations to microbial growth, and this may explain the NO_3^- accumulation commonly observed in semi-arid, arid, and Mediterranean ecosystems. We examined linkages between soil C availability and gross N cycling rates during summer in three common semiarid vegetation types: sagebrush, crested wheatgrass, and cheatgrass. To determine whether dry soils inhibit microbial colonization of plant detrital inputs, we stimulated soil C availability *in situ* by killing plant biomass shortly before the summer dry-season with herbicide (detrital-pulse treatment). Soil C and gross N cycling rates were determined during field incubations of intact soil cores from untreated soils on three occasions from late spring to late summer, and from detrital-pulse treated soils on two occasions in summer. We hypothesized that greater C availability, resulting in increased microbial biomass and C mineralization rates, would translate to greater N immobilization rates, and this would inhibit the

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accumulation of inorganic N during summer months.

There were few differences in soil C and N cycling among vegetation types. In all vegetation types, the *in situ* detrital-pulse stimulated soil C mineralization and gross N cycling rates compared to untreated soils; however, this treatment did not inhibit the summertime accumulation of NO_3^-. Instead, elevated N cycling rates and large labile N pools in detrital-pulse soils persisted throughout the summer. Our results combined with a model of microbial C-N dynamics indicate that microbes in detrital-pulse soils were utilizing substrates with C:N ratios 27% lower than in untreated soils ($p<0.04$), and were much lower than expected based on the C:N of plant detritus. This suggests that substrates released by senescing plants had much lower C:N than would be predicted based on the overall C:N of plant tissue. In addition, appearance of ^{15}N in different soil density fractions showed that the detrital-pulse treatment stimulated microbial N immobilization in both C-rich and N-rich soil microsites. Greater N immobilization associated with light fraction organic matter is consistent with greater microbial growth due to earlier input of plant detritus. Interestingly, heavy fraction organic matter was also an important sink for immobilized N and was strongly stimulated by the detrital-pulse treatment, indicating that this fraction is not as recalcitrant as formerly thought.

INTRODUCTION

The supply of plant carbon (C) inputs to soil, through leaf and root turnover, is an important source of labile C substrate that drives the growth and activity of heterotrophic soil microorganisms. The activity of heterotrophic microbes is a key linkage between soil C and nitrogen (N) cycling. Consumption of labile C results in microbial growth and

immobilization of available N (Hart et al., 1994; Gallardo and Schlesinger, 1995; Schaeffer and Evans, 2005). Simultaneously, in comparatively N-rich microsites, microbial intra- and extracellular enzyme activity and biomass turnover results in the release (or mineralization) of actively cycled N (Bengtsson et al., 2003; Schimel and Weintraub, 2003; Saetre and Stark, 2005). The size of microbial biomass pools and rates of N immobilization have been linked to soil C availability across broad climate gradients (Barrett and Burke, 2000; Booth et al., 2005), beneath plant canopies versus plant-interspaces (Barrett and Burke, 2000; Chen and Stark, 2000), and after experimental additions of plant detritus (Recous et al., 1999; Whalen et al., 2001; Luxhoi et al., 2006).

Shifts in the dominant vegetation type may alter soil C availability through differences in the quantity and quality of plant detrital inputs (Vinton and Burke, 1995; Evans et al., 2001; Carrera et al., 2003), particularly in semiarid ecosystems where soil organic C and N pools are small (Schlesinger, 1997). Increased C inputs, through differences in foliage and root turnover among different vegetation types (Caldwell et al., 1977; Gill and Jackson, 2000; Belnap and Phillips, 2001; Schenk and Jackson, 2002), may increase microbial N demand and reduce N available for plant uptake (Hart et al., 1994). By contrast, increased quality of plant detrital inputs (i.e. lower litter C:N ratios) may result in greater N availability due to decreased microbial demand for inorganic N per unit organic C consumed (Hart et al., 1994; Chen and Stark, 2000; Carrera et al., 2003; Saetre and Stark, 2005).

The simultaneous occurrence of N mineralization and N immobilization in bulk soils suggests that microbes are distributed among distinct microsites dominated by N-rich (C-limited) and C-rich (N-limited) substrates (Chen and Stark, 2000). While the

source of mineralizable N is believed to be derived predominantly from older, more highly decomposed mineral-associated organic matter with narrow C:N ratios, such as the heavy fraction (HF), C-rich microsites with high rates of microbial N consumption are likely to be associated with particulate organic matter derived from plant detritus, such as the light fraction (LF) (Sollins et al., 1984; Boone, 1994; Crow et al., 2007). Immobilization of added ^{15}N into soil organic matter fractions, in combination with determination of gross N cycling rates, may better reveal the effects of small changes in the quantity or quality of plant detrital inputs to soil compared to rates estimated for bulk soils alone.

In semiarid ecosystems, soil C and N cycling may also be affected by the timing of plant biomass turnover relative to seasonal patterns of temperature and soil moisture. As the summer dry-season develops, perennial plants reduce growth rates, increase litterfall (West and Fareed, 1973; Comstock and Ehleringer, 1992; Evans and Black, 1993), and shift the distribution of active roots to deeper soil depths (Fernandez and Caldwell, 1975). By contrast, annual grasses senesce with the onset of the summer dry-season (Stewart and Hull, 1949; Harris, 1967). In these soils, soil C availability would be expected to increase during the early summer due to the pulse of high C:N leaf and root litter inputs. In spite of this, surface soils of semiarid ecosystems tend to accumulate NO_3^- during the summer (Jones and Woodmansee, 1979; Jackson et al., 1988; Davidson et al., 1990; Augustine and McNaughton, 2004), particularly in annual grass soils (Booth et al., 2003; Sperry et al., 2006; Hooker et al., 2008). This NO_3^- accumulation suggests that microbial N immobilization is limited by C availability, which is inconsistent with the expectation that plant detrital inputs stimulate soil C availability. One explanation for

this inconsistency is that by the time annual grasses senesce in late spring (late-May to early-June), the soil may already be too dry for microbes to colonize the newly released detritus. Thus, there may be a time-lag in N immobilization because microbes are unable to colonize plant detritus until soil moisture increases in autumn.

In this study we investigated whether the apparent summertime C limitation in semiarid soils, evidenced by NO_3^- accumulation, was due to a time-lag in microbial colonization and decomposition of recently released plant detritus. Gross N cycling rates and soil C availability were compared among three distinct vegetation types common to the Great Basin: Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), introduced perennial crested wheatgrass (*Agropyron desertorum*), and invasive annual cheatgrass (*Bromus tectorum*) communities. We stimulated soil C availability *in situ* by releasing plant biomass to the soil detrital pool three weeks prior to the summer dry-season, using large soil cylinders and herbicide at peak biomass; this is referred to as the detrital-pulse treatment. Since only a fraction of perennial plant root biomass turns over annually (Gill and Jackson, 2000), the detrital-pulse treatment likely increased the quantity of plant detrital inputs in perennial plant-dominated systems, but only the timing of plant detrital inputs should be affected in the annual grass system. We hypothesized that the detrital-pulse treatment would stimulate C availability and increase microbial biomass and C mineralization rates, and thus result in higher gross N immobilization rates compared to untreated soils. This study is novel in that we investigated the response of soil microbial C and N dynamics to an *in situ* pulse of plant detritus, and used ^{15}N to link gross N immobilization rates to organic matter density fractions.

MATERIALS AND METHODS

Study site

This study was carried out on a Great Basin sagebrush rangeland in Rush Valley (Tooele County), Utah (112˚ 28' W, 40˚ 17' N, elev. 1610 m). The site contains extensive, nearly monodominant stands of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young), crested wheatgrass (*Agropyron desertorum* (Fisch. ex. Link), var. 'Nordan'), and cheatgrass (*Bromus tectorum* L.). Mean annual precipitation and temperature measured on-site over a 5-year period were 240 mm and 8.3˚C, respectively. The summer dry-season begins in early June as mean monthly precipitation declines from spring (29.4 mm for a 5-year average) to summer (15.7 mm). Most summer precipitation occurs as small events (>75% of summer precipitation events are <5 mm), while larger, more biologically effective pulses are uncommon (>5 mm occur approximately 1.0 ± 0.1 days/month; >15 mm events occur 0.2 ± 0.2 days/month). Soils at the site are derived from lacustrine and alluvial sediments of primarily limestone deposits, and classified as silt loam, very deep, well drained, fine-silty, mixed, superactive, mesic Typic Calcixerolls (A. Mitchell *personal communication*; Trickler et al., 2000). Soils contain approximately 10 g CO_3-C kg^{-1} soil in the surface 0-10 cm, and are non-saline (EC < 2.0 dS/m).

Stands of crested wheatgrass and cheatgrass were established in 1992 on areas formerly dominated by sagebrush. Crested wheatgrass was established to improve rangeland quality by disking to remove shrubs and drill-seeding (30-cm row spacing). Cheatgrass established naturally with the onset of autumn rains after a summer wildfire

consumed several large areas of sagebrush. In late 1998, four 22 x 22 m permanent plots were created in each vegetation type. Permanent plots were randomly located along two north-south and two east-west transects that crossed all three vegetation types.

Installation of the detrital-pulse treatment and field sampling

On May 4, 2003, approximately 3 weeks prior to the onset of the summer dry-season, ten random locations within each plot were permanently marked. The detrital-pulse treatment was initiated at five of the sampling points by inserting a 30-cm diameter x 25-cm long cylinder into the soil, severing all roots. An area within and around (0.5-m radius) the cylinder was sprayed with herbicide (Roundup, Monsanto) to kill the vegetation and release plant biomass to the soil as detritus. The remaining five sampling points at each plot were left as untreated soils, and were at least 2 m from a detrital-pulse treatment. For sagebrush plots, we used only areas beneath shrub canopies; untreated and detrital-pulse plots were placed beneath separate shrubs, but with similar aspect in relation to the shrub stem. All aboveground vegetation appeared to be dead within the detrital-pulse plots approximately 10 d after herbicide application, with the exception of sagebrush shrubs. We sampled untreated plots in late May, and both plot types in late June and early September (Table 3-1). A fourth sampling date was planned for mid-autumn, after the onset of autumn rains, but soils froze soon after 15 mm of precipitation fell in November.

Soil sampling consisted of core collection and field incubation of intact cores to determine C mineralization and gross N cycling rates using ^{15}N isotope pool dilution (Stark, 2000). Within each plot, six cores (4.8-cm diameter x 10-cm deep) were collected

from both untreated and detrital-pulse treated sampling points after all surface litter was removed; different sampling points were used on each sampling date. Three pairs of cores were injected, using a side-port injection needle, with eight 1-mL additions of: 1) $(^{15}NH_4)_2SO_4$ (99 atom% ^{15}N), 2) $K^{15}NO_3$ (99 atom% ^{15}N), or 3) dilute K_2SO_4 having the same ionic strength as the average of the $^{15}NH_4^+$ and $^{15}NO_3^-$ solutions (Table 3-2). The $^{15}NH_4^+$-amended cores were used to measure gross N mineralization, $^{15}NO_3^-$-amended cores were used for gross nitrification, and water (dilute K_2SO_4) amended cores were used for unstimulated (i.e. no inorganic N added) net N mineralization rates (described below). Injections increased soil moisture by approximately 0.04 g H_2O g^{-1} soil. The concentration of added $^{15}NH_4^+$ was 31.3 μg N mL^{-1} for all sampling dates. The $^{15}NO_3^-$ concentrations were 25.0 μg ^{15}N mL^{-1} for the May and June sampling dates. Since NO_3^- concentrations increase during the summer dry-season, particularly in cheatgrass soils (*unpublished data*, see also Booth et al., 2003), the concentration of $^{15}NO_3^-$ added was increased to 37.5 μg ^{15}N mL^{-1} for crested wheatgrass and sagebrush soils, and 125.0 μg ^{15}N mL^{-1} for cheatgrass soils in September. Concentrations of ^{15}N added to untreated and detrital-pulse soils were the same. After each pair of cores was injected, one core from each pair was homogenized and a subsample (25-g dry weight) was extracted with 200 mL of 2M KCl in the field. The remaining cores were placed in 1-L canning jars with septa-lids, buried upright, and covered with 2.5-cm soil.

After 48 hours of *in situ* incubation, headspace gas was sampled to determine the C mineralization rate. A 30-mL sample of headspace gas was collected and injected into evacuated 13-mL vials; CO_2 blanks were obtained from jars incubated without soil. Soil cores were removed from jars, homogenized, and subsamples were extracted with KCl in

the field, as described above. Additional subsamples from incubated cores were collected to determine microbial biomass C and N using chloroform fumigation-extraction (Haubensak et al., 2002); values are reported as C- and N-flush. Briefly, paired subsamples (20-g dry weight) were either extracted with 200 mL 0.5 M K_2SO_4, or placed in 50-mL beakers in a glass vacuum desiccator containing 30-mL ethanol-free chloroform. Chloroform fumigation involved evacuation and flushing the desiccator three times, using a hand-pump in the field. The desiccator was transported back to the laboratory, and after 72 h of fumigation, samples were extracted with 0.5 M K_2SO_4, as described above. During soil extraction, all samples were shaken for 45 min. and stored in a cold-room at 4˚C overnight. Soil extracts were filtered with pre-leached Whatman #4 filters. Soil residues remaining on filters following KCl extraction were dried for 72 h at 70˚C. These samples were used to separate soil organic matter into particle density fractions (described below). Additional subsamples of all harvested soils were used to determine gravimetric moisture content by mass-loss after 48 h at 105˚C.

Headspace CO_2 concentrations were analyzed with a Varian 3300 gas chromatograph (TCD detector, Varian Instruments, Walnut Creek, CA, USA). Soluble organic C concentrations in K_2SO_4 extracts were analyzed with Phoenix 8000 TOC analyzer (Teledyne-Tekmar, Mason, OH, USA). Concentrations of soil NH_4^+ and NO_3^- (2 M KCl), and total soluble N (0.5 M K_2SO_4) following persulfate oxidation (Cabrera and Beare, 1993), were analyzed colorimetrically with a Lachat AE flow-injection autoanalyzer (Lachat Instruments, Milwaukee, WI, USA). The NH_4^+ and NO_3^- in soil KCl extracts were diffused onto acidified filter paper disks for determination of ^{15}N atom percent enrichment by mass spectrometry following the procedure described in Stark and

Hart (1996).

Soil residues, obtained following KCl extraction of ^{15}N amended soils, were sieved (< 1 mm) and then separated into three density fractions using a procedure modified from Magid et al. (2002). Approximately 12 g of dry soil residue were placed in 50-mL centrifuge tubes with 30 mL of sodium hexametaphosphate (HMP, 5 g L^{-1}, $\rho \sim 1.0$ g cm^{-3}), shaken for 30 min., and then centrifuged at 2100 rpm (900 x g). The floating light fraction (LF, $\rho \leq 1.0$ g cm^{-3}) material was collected by decanting the supernatant onto a Falcon bottle-top filter unit (part no. 357105, Becton-Dickinson, Franklin Lakes, NJ, USA) holding a pre-weighed Fisher G6 glass fiber filter. Previous work found no difference in C or N concentrations when density fractions from these soils were decanted compared to collected with a pipette (*unpublished data*). The pellet was re-suspended with fresh HMP solution, and the procedure repeated twice more. Medium fraction organic matter (MF, $1.0 < \rho \leq 1.70$ g cm^{-3}) was then collected by re-suspending the pellet with 30 mL of sodium polytungstate ($\rho = 1.70$ g cm^{-3}; Sometu, Van Nuys, CA, USA), and the same process repeated twice using a second Falcon filter unit. The remaining pellet contained the heavy fraction organic matter (HF, $\rho > 1.70$ g cm^{-3}). Residual sodium polytungstate was removed from the heavy fraction by re-suspending the pellet in deionized water, and shaking, centrifuging and decanting two more times. Glass fiber filters containing LF and MF, and centrifuge tubes containing HF, were dried at 70˚C for 48 h, and weighed. Light and medium fraction materials were then carefully scraped off the filters, and ground with a mortar and pestle. Subsamples of LF and MF were wrapped in 8x5 mm tin capsules, for C and N elemental and ^{15}N isotopic analysis with a Europa 20/20 SL isotope ratio mass spectrometer (Sercon, Cheshire, U.K.). Heavy

fraction C, N, and ^{15}N analyses were performed after removal of inorganic C using the HCl fumigation method of Harris et al. (2001).

Calculation of gross N transformation rates

Gross rates of NH_4^+ and NO_3^- production (mineralization and nitrification, respectively) were calculated from the dilution and disappearance of ^{15}N-enriched product pools following the isotope dilution methodology described in Stark (2000). Gross NH_4^+ and NO_3^- consumption rates were calculated as:

Gross consumption rate = Gross production rate – net production rate (1)

Addition of ^{15}N solutions may stimulate gross N consumption rates if N is limiting (Davidson et al., 1991). Stimulated rates of NH_4^+ and NO_3^- consumption were calculated using data from soil cores that had received ^{15}N additions. To calculate unstimulated consumption rates, we used net production rates from cores that received only the dilute K_2SO_4 solution. Dilute K_2SO_4 was used instead of deionized water to account for potential confounding effects of solution ionic strength on net rates. Gross NH_4^+ immobilization was calculated as:

Gross NH_4^+ immobilization = Gross NH_4^+ consumption – Gross nitrification (2)

using both stimulated and unstimulated NH_4^+ consumption rates. Since stimulated rates of nitrification (after $^{15}NH_4^+$ addition) were not determined in this study, stimulated NH_4^+ immobilization may be overestimated if nitrification was also stimulated by $^{15}NH_4^+$ addition.

Rates of N immobilization into soil organic matter density fractions were calculated based on the appearance of ^{15}N in the organic matter fractions, after correcting

for initial (T0) ^{15}N content and declining ^{15}N enrichment of the source pool, following Davidson et al. (1991):

$$M_{AB} = \frac{P_{Bt} \cdot (E_{Bt} - E_{B0})}{E_{A0} \cdot (1 - e^{-k}) / k} \Big/ t \quad (3)$$

where M_{AB} is the N immobilization rate from source pool A to organic matter fraction B, P is the pool size of the organic matter sink, E is the ^{15}N atom percent excess of source and sink pools, k is the decay constant of source pool ^{15}N, where $k = \ln(E_{A0}/E_{At})/t$, and t is time in days.

Statistical analysis

Soil C and N pools and cycling rates were compared among vegetation types and sampling dates using the Proc Mixed procedure (SAS version 9.0, Cary, NC). Vegetation type and date were fixed factors, and plot was a random effect. Comparisons between untreated and detrital-pulse treatments used data only from the June and September sampling dates. The split-plot design for the error covariance matrix was used, based on AICC and BIC information criteria. The SLICE command was used to evaluate significant differences among vegetation types and/or detrital-pulse treatments for each sample date. Patterns between N production and consumption rates among vegetation types were examined with ANCOVA using the same model structure as above. Statistical differences were considered significant for $\alpha = 0.05$.

RESULTS

Sampling date and vegetation type effects – untreated soils

Sampling date had strong effects on soil C and N cycling in this study, likely due to an early summer storm that temporarily increased soil moisture to field capacity and reduced soil temperatures prior to the June sampling (Table 3-1). This 25-mm precipitation pulse increased C mineralization rates by 50% and microbial biomass C and N by 150% and 240%, respectively, and reduced soluble organic C and N concentrations by nearly 50%, compared to the drier May and September sampling dates (Table 3-3). Vegetation type had no significant main effect ($p>0.05$) for these variables. Gross N mineralization rates averaged 2.31 mg N kg^{-1} soil day^{-1} across all soils, and nitrification consumed approximately 26% of mineralized NH_4^+ (0.61 mg N kg^{-1} soil day^{-1}) (Table 3-4). Average rates of NH_4^+ and NO_3^- production and consumption did not differ significantly among sampling dates or vegetation types.

While $^{15}NO_3^-$ addition did not affect N cycling rates, addition of $^{15}NH_4^+$ during isotope dilution measurements strongly affected rates compared to water additions (dilute K_2SO_4). Addition of $^{15}NH_4^+$ resulted in negative net ammonification (-0.66 mg N kg^{-1} soil day^{-1}) that was approximately balanced by net nitrification (0.73 mg N kg^{-1} soil day^{-1}), while positive net ammonification and net nitrification rates (0.32 and 0.28 mg N kg^{-1} soil day^{-1}) were observed when no N was added. Addition of $^{15}NH_4^+$ increased initial NH_4^+ pools by 80% (May) to 44% (September) (Tables 3-2 and 3-3), and this resulted in significant stimulation of gross NH_4^+ consumption (+50%, $p<0.001$) and immobilization (+72%, $p<0.001$) rates in untreated soils (Table 3-4). The $^{15}NO_3^-$

additions increased initial NO_3^- pools by 377% (May) to 41% (September) (see Tables 3-2 and 3-3), but NO_3^- consumption rates were only marginally stimulated ($p=0.065$) when soils were moist in June. NO_3^- consumption accounted for approximately 19% of total N immobilization in these soils.

Effects of detrital-pulse treatment

The detrital-pulse treatment increased soil C availability relative to untreated soils, presumably due to the addition of plant detritus as substrate for soil microbes. C mineralization rates were 28% greater in detrital-pulse than untreated soils in June ($p=0.025$; Table 3-5), but only 9% greater in September ($p=0.49$). Detrital-pulse soils also had greater microbial biomass C (+13%) and N (+46%) flushes compared to untreated soils, but the difference was significant only for the microbial N-flush ($p=0.007$). The effects of the detrital-pulse treatment were greater in June than September, and there was no significant vegetation x pulse-treatment interaction.

In contrast to the expected decline in inorganic N pools in detrital-pulse soils, extractable N pools (organic N, NH_4^+, and NO_3^-) were significantly greater in the detrital-pulse treatment (Table 3-5). Extractable organic N pools increased by 68% ($p<0.001$), while NH_4^+ ($p<0.0001$) and NO_3^- ($p<0.0001$) pools were 250% and over 700% greater.

Gross N cycling rates were significantly greater in detrital-pulse vs. untreated soils across all vegetation types and both June and September sampling dates (Table 3-4). Gross N mineralization increased by 230%, and gross nitrification rates increased by 500% ($p<0.0001$ for both). Unstimulated rates of gross NH_4^+ consumption, NH_4^+ immobilization, and NO_3^- consumption increased by 260%, 170%, and 220% in detrital-

pulse compared to untreated soil (Table 3-4). In detrital-pulse soils, there was no significant stimulatory effect of $^{15}NH_4^+$ and $^{15}NO_3^-$ additions on N consumption or immobilization rates ($p>0.20$ for all).

N immobilization in soil organic matter density fractions

Substantial amounts of added ^{15}N were immobilized and recovered in soil organic matter fractions (LF, MF, and HF) during the 48-h incubations, particularly in June (Figure 3-1). While the light and medium fractions accounted for only a small proportion of soil mass (Table 3-6), they accounted for over 50% of N immobilization associated with soil organic matter fractions when expressed per unit C. Neither the mass nor the C and N concentrations of soil organic matter fractions differed significantly among vegetation types, sampling dates, or between untreated and detrital-pulse soils ($p>0.20$ for all main effects). There was 150 to 300% greater immobilization of NH_4^+ than NO_3^- in LF and HF organic matter, while rates were similar among N forms in the MF. Detrital-pulse soils had greater N immobilization into LF and HF than untreated soils ($p=0.014$, and $p=0.003$, respectively), but MF immobilization rates did not differ between soil treatments ($p=0.18$) (Figure 3-1). Differences between treatments were greater in June than in September, and were due to greater immobilization of NH_4^+ rather than NO_3^-.

DISCUSSION

This study reveals some important gaps in our understanding of the nature of organic matter release from plant detritus. While the *in situ* detrital-pulse treatment stimulated soil C availability and gross N consumption rates compared to untreated soils,

this treatment did not inhibit the summertime accumulation of NO_3^- in surface soils. Instead, inorganic N pools were 3 to 5 times greater in soils receiving the detrital pulse than in untreated soils. One reason for this change was that the relative stimulation of gross N cycling (68 to 700%) by the detrital-pulse treatment was greater than the relative increase in C availability (28%) (Figure 3-2), and N cycling rates remained elevated through September.

Other studies have reported net N release in soil after addition of detritus, notably studies of root decomposition (Seastedt et al., 1992; Parton et al., 2007). Two important factors that regulate whether microbial consumption of organic matter results in N release (mineralization) or assimilation of additional inorganic N (immobilization) are: 1) the amount of microbial biomass growth per unit substrate consumed (substrate use efficiency, SUE), and 2) the C:N ratio of the substrate consumed. In a recent study, Parton et al. (2007) suggest that the linear release of N from grass roots over time was due to greater availability of soil moisture, labile organic matter, and nutrients to microbes decomposing root versus surface leaf litter. However, all of these conditions would be expected to increase microbial substrate use efficiency (see del Giorgio and Cole, 1998; Six et al., 2006), and this would result in greater N immobilization rather than N mineralization. It seems more likely that the net N release from added detritus reported by Parton et al. (2007) and observed in this study is due to the release of substrates with lower C:N ratios.

Unfortunately, the C:N ratio of substrates utilized by soil microbes cannot be measured directly. However, we can estimate substrate C:N by modeling microbial C and N dynamics (Saetre and Stark, 2005). For soils in June, when microbial uptake of

detrital substrates should be high, we estimate that the substrate use efficiency was greater in detrital-pulse (77%) than untreated soils (62%) (Table 3-7), following the method of Schimel (1988). These estimates assume that new microbial growth has the same stoichiometry as the overall microbial C:N, and that inorganic N is the sole source of N for growth. These values are reasonable given that soils in June were moist and warm, and are consistent with greater availability of labile substrates in detrital-pulse versus untreated soils. Applying our soil C and N cycling data to the model developed by Saetre and Stark (2005), we calculate that microbes in detrital-pulse soils were consuming substrates with C:N ratios approximately 27% lower than in untreated soils ($p=0.04$) (Table 3-7). These C:N ratios are substantially lower than expected based on measurements of plant foliage (51.7 ± 4.5) and fine root (26.6 ± 2.5) tissue from cheatgrass, crested wheatgrass, and sagebrush vegetation (see Chapter 2). Thus, rather than releasing substrates with high C:N ratios and promoting net microbial N immobilization, the detrital-pulse treatment apparently released labile substrates with low C:N ratios during the early stages of decomposition, and microbial utilization of these substrates stimulated net N mineralization compared to untreated soils.

Results from soil laboratory incubations with plant residues amendments suggest that temporal changes in C and N cycling after residue incorporation reflect differences in the C and N stoichiometry of substrates utilized by microorganisms (Trinsoutrot et al., 2000a; Jensen et al., 2005; Bruun et al., 2006). Soluble components of plant detritus may be released during the early stages of decomposition, while plant polymers (such as cellulose) with higher C:N ratios are degraded more slowly during later stages of decomposition. To our knowledge, there are no reports in the literature comparing the

bulk C:N ratio of added substrates against estimates of C:N of substrates utilized by soil microbes with which to compare our results. Most studies have focused on decomposition of aboveground rather than belowground plant tissues, however, there may be important differences in microbial C and N dynamics during decomposition of aboveground versus belowground tissues (Trinsoutrot et al., 2000b; Bird and Torn, 2006; Parton et al., 2007; Bird et al., 2008). In addition, we are aware of no other studies examining soil microbial C and N cycling in response to an *in situ* pulse of plant detritus. Other studies apply aboveground or belowground materials to homogeneously mixed soils and often add large inorganic N amendments (for example, Recous et al., 1999; Jensen et al., 2005), however, this may alter the spatial distribution of low and high C availability microsites and stimulate microbial C and N cycling rates relative to intact soils (Luxhoi et al., 2004; Booth et al., 2006; Magid et al., 2006).

Besides stimulating the release of labile substrates with low C:N ratios, the detrital-pulse treatment stimulated microbial activity in both C-rich and N-rich soil organic matter fractions. In moist June soils, N immobilization rates associated with light fraction organic matter were twice as high in detrital-pulse compared to untreated soils (Figure 3-1); this is consistent with our expectation that earlier release of plant detritus would stimulate greater microbial growth. Other studies have found light fraction organic matter to be a significant sink for immobilized N (Recous et al., 1999; Whalen et al., 2001; Compton and Boone, 2002). By contrast, heavy fraction organic matter, with narrow C:N ratios (Table 3-6), is generally considered to be a source of inorganic N rather than a sink (Boone, 1994; Whalen et al., 2000). However, we observed that heavy fraction organic matter immobilized twice as much N in the detritus pulse treatment. This

suggests that heavy fraction organic matter is an important sink of immobilized N and is sensitive to recent organic matter additions. Thus, at least a portion of C in heavy fraction is relatively labile (see Swanston et al., 2002, 2005; Crow et al. 2006), and not as recalcitrant as formerly thought.

The lack of significant differences in soil C and N cycling rates among vegetation types in this study is surprising. While we are currently unable to explain this result, it may be that microbial access to labile organic matter during the summer dry-season is similarly limited by low soil moisture availability among vegetation types. Moreover, differences in soil organic matter and root biomass among vegetation types were small (*see* Chapter 2; Tables 2-2 and 2-3). In annual grass soils, the detrital-pulse treatment affected only the timing of detrital inputs, but in perennial plant-dominated systems both the quantity and timing of plant inputs were affected. The similar response to the detrital-pulse among vegetation types implies that the timing of plant detrital inputs was more important the relative quantity of inputs in this semiarid ecosystem.

The detrital-pulse treatment also eliminated plant N uptake, however, previous work indicates little net N accumulation in annual or perennial plants from early May to June (<5.7 kg N ha^{-1} over 6 weeks, see Figure A-4), and this amount of plant N uptake would account for less than 20% of the difference in labile N between untreated and detrital-pulse soils in June. While perennial plants in semiarid ecosystems may take up N in response to precipitation pulses, senescent cheatgrass plants do not (Bilbrough and Caldwell, 1997; Ivans et al., 2003). In this study, cumulative precipitation from the time that the detrital-pulse treatment was initiated to the June sampling date (but prior to the large precipitation event) was only 3.8 mm over 44 days; thus it is unlikely that N uptake

by perennial plants was significant during this period.

In summary, the timing of plant detrital inputs to soil has a significant effect on soil C and N availability in this semiarid ecosystem. Earlier release of plant biomass to soil detrital pools stimulated N availability to a greater extent than C availability relative to untreated soils, such that the results from this *in situ* study could not be predicted based on the C:N ratio of plant biomass. We also observed that the detrital-pulse treatment stimulated microbial N immobilization rates in both C-rich and N-rich soil organic matter fractions. While greater N immobilization in the C-rich light fraction is consistent with greater microbial growth associated with earlier release of plant detritus, greater N immobilization in the N-rich heavy fraction suggests that at least a portion of C in this organic matter fraction is relatively labile, and therefore is not as recalcitrant as formerly thought. Further work that focuses attention on the release and microbial utilization of substrates derived from plant detritus is needed in order to better predict the response of biogeochemical C and N cycling to major disturbances, such as changes in dominant vegetation type.

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Table 3-1. Field conditions during treatment installation and soil sampling dates

Date	soil H_2O (g g^{-1})	Air temp. (˚C)	Soil temp. (˚C at 10-cm)	14-day antecedent precipitation (mm)
4 May, 2003 (initiate treatment)	0.150	4.7	8.5	24.0
28 May, 2003	0.082	24.6	23.1	0.3
25 June, 2003	0.020	15.7	18.5	24.9 *
5 September, 2003	0.071	19.8	22.8	6.6

Cheatgrass was in the early flowering stage in early May, in seed-maturation (early senescence) stage in late May, and completely senesced by June.

Crested wheatgrass was in the vegetative growth stage throughout May, and flowering in June; by September, plants were largely dormant.

Sagebrush plants had initiated leaf and stem growth in early May, and flowering spikes were growing in June.

* Cumulative precipitation from late-spring to early-summer was 3.8 mm over 44 days prior to the large June precipitation event.

Table 3-2. Concentrations of ^{15}N added and % increase in T0 NH_4^+ and NO_3^- pools during isotope dilution measurements

Treatment	Solution: Date	NH_4^+ mg ^{15}N kg^{-1} added	NH_4^+ % T0 pool increase	NO_3^- mg ^{15}N kg^{-1} added	NO_3^- % T0 pool increase	water (mM K_2SO_4)
Untreated	May	1.3	80	1.0	377	1.2
	June	1.3	68	1.0	63	1.2
	Sept.	1.3	44	4.8, 1.5 †	47, 39 †	1.5
Detrital-pulse	June	1.3	16	1.1	9	1.2
	Sept.	1.3	17	4.8, 1.5 †	9, 8 †	1.5

† $^{15}NO_3^-$ additions differed among vegetation types, cheatgrass soils received 4.8 mg ^{15}N kg^{-1} soil, and crested wheatgrass and sagebrush soils received 1.5 mg ^{15}N kg^{-1} soil, due to previous observations of larger NO_3^- pools in cheatgrass soils.

Table 3-3. Characteristics of labile soil C and N pools in untreated soils

Date	Veg. type	C min. rate	Microbial biomass C-flush	Microbial biomass N-flush	Soluble organic C	Soluble organic N	NH_4^+	NO_3^-
		mg C kg^{-1} day^{-1}	mg C kg^{-1}	mg N kg^{-1}	mg C kg^{-1}	mg N kg^{-1}	mg N kg^{-1}	mg N kg^{-1}
May	Cheatgrass	5.55 (0.53) **a**	88.9 (16.2)	10.6 (1.2)	350.3 (46.1)	24.9 (1.4)	1.5 (0.2)	0.4 (0.1)
	Crested wheatgrass	3.54 (0.38) **b**	67.7 (11.6)	10.9 (0.6)	306.0 (13.8)	24.8 (1.9)	2.2 (0.1)	0.5 (0.1)
	Sagebrush	3.42 (0.36) **b**	84.2 (16.6)	13.2 (1.5)	353.9 (86.0)	26.6 (7.1)	1.8 (0.5)	0.7 (0.5)
	Average	**4.17 (0.51) B**	**80.2 (8.3) C**	**11.6 (0.7) C**	**336.7 (30.4) A**	**25.4 (2.3) A**	**1.8 (0.1) B**	**0.5 (0.2) C**
June	Cheatgrass	4.96 (0.44)	275.6 (41.5)	47.4 (5.2)	135.6 (19.0) **b**	11.5 (1.5)	3.0 (0.3)	1.1 (0.4)
	Crested wheatgrass	5.71 (0.47)	324.5 (33.4)	65.5 (10.0)	148.9 (6.7) **b**	15.1 (3.1)	2.9 (0.4)	2.0 (0.3)
	Sagebrush	5.92 (0.57)	397.4 (15.7)	57.3 (3.4)	269.7 (66.6) **a**	17.3 (3.6)	3.4 (0.9)	1.2 (0.1)
	Average	**5.53 (0.50) A**	**332.5 (22.5) A**	**56.7 (4.2) A**	**184.7 (27.8) B**	**14.6 (1.7) B**	**3.1 (0.1) A**	**1.5 (0.2) B**
Sept.	Cheatgrass	1.96 (0.12)	159.9 (38.8)	21.6 (1.9)	171.2 (17.2) **b**	20.4 (1.0)	2.8 (0.2)	9.5 (1.0) **a**
	Crested wheatgrass	2.26 (0.15)	216.5 (31.4)	21.0 (2.2)	168.6 (13.8) **b**	33.1 (5.3)	4.1 (0.3)	4.4 (0.7) **b**
	Sagebrush	3.01 (0.27)	172.7 (19.5)	21.6 (2.1)	309.6 (25.2) **a**	19.5 (2.8)	2.9 (0.5)	4.6 (1.2) **b**
	Average	**2.41 (0.23) C**	**183.0 (17.7) B**	**21.4 (1.1) B**	**208.0 (21.1) B**	**24.3 (2.6) A**	**3.3 (0.1) A**	**6.2 (0.9) A**
Significant effects from mixed ANOVA (p-values)								
	Sampling Date	0.0002	<0.0001	<0.0001	<0.0001	<0.0001	<0.004	<0.0001
	Vegetation type	n.s.	n.s.	n.s	0.08	n.s.	n.s.	n.s.
	Date x Veg.	0.015	n.s.	n.s.	0.11	0.07	n.s.	0.06

Data are means with standard error in parentheses; lowercase letters indicate significant differences among vegetation types within a sampling date, uppercase letters indicate differences among sampling dates ($p \leq 0.05$).

Table 3-4. Gross N cycling rates in untreated and detrital-pulse soils

		Soil treatment		
		All dates	June and September only †	
Gross N cycling rate		Untreated	Untreated	Detrital-pulse
N mineralization		2.31 (0.21)	2.38 (0.29)	7.88 (1.60)
NH_4^+ consumption	Unstimulated	1.98 (0.29)	2.45 (0.34)	8.95 (1.88)
	Stimulated	2.97 (0.19) ***	3.08 (0.29) ***	8.75 (1.58)
NH_4^+ immobilization	Unstimulated	1.37 (0.29)	1.78 (0.42)	5.82 (1.59)
	Stimulated	2.36 (0.20) ***	2.42 (0.33) ***	4.74 (1.83)
Nitrification		0.61 (0.12)	0.69 (0.20)	4.13 (1.41)
NO_3^- consumption	Unstimulated	0.33 (0.16)	0.50 (0.17)	1.62 (0.52)
	Stimulated	0.53 (0.16)	0.58 (0.20)	2.64 (0.81)
N immobilization	Unstimulated	1.71 (0.36)	2.28 (0.48)	7.51 (1.51)
	Stimulated	2.89 (0.26) **	3.00 (0.25) **	7.52 (1.86)

Data are means across sampling dates and vegetation types, expressed as mg N kg^{-1} soil day^{-1}, with standard error in parentheses.

All N cycling rates in detrital-pulse soils were significantly greater than untreated soils, but rates did not differ significantly among vegetation types or sampling dates (see text).

† Values for untreated soils from June and September are presented for comparison with detrital-pulse soils.

Asterisks indicate a significant difference between stimulated and unstimulated N consumption rates (* $p<0.05$; ** $p<0.01$, *** $p<0.001$).

Table 3-5. Characteristics of labile soil C and N in untreated and detrital-pulse soils

Date	Treatment	Microbial biomass C min. rate	Microbial biomass C-flush	Microbial biomass N-flush	Soluble organic C	Soluble organic N	NH_4^+	NO_3^-
June	Untreated	5.53 (0.50)	332.5 (22.5)	56.7 (4.2)	184.7 (27.8)	14.6 (1.7)	3.1 (0.3)	1.5 (0.2)
	Detrital-pulse	7.07 (0.84) *	375.5 (27.5)	82.8 (9.2) ***	201.8 (32.0)	24.5 (3.6) ***	10.7 (1.5) ***	14.6 (2.8) ***
Sept.	Untreated	2.41 (0.23)	183.0 (17.7)	21.4 (1.1)	204.0 (20.5)	24.3 (2.6)	3.3 (0.3)	6.2 (0.9)
	Detrital-pulse	2.62 (0.31)	177.9 (12.2)	25.3 (2.6)	211.3 (16.7)	27.4 (2.6)	11.6 (1.6) ***	33.2 (5.5) ***
Significant effects from mixed ANOVA (p-values)								
Sampling date		0.0007	0.0004	<0.0001	n.s.	<0.0001	n.s.	<0.0001
Vegetation type		n.s.	n.s.	n.s.	0.02 †	n.s.	n.s.	n.s.
Detrital trtmt		0.039	n.s.	0.007	n.s.	0.0006	<0.0001	<0.0001
Detrital trtmt x Date		n.s.	n.s.	n.s.	n.s.	0.047	n.s.	0.027

Data are means with standard error in parentheses (n=12).

Units are mg C kg $soil^{-1}$ day^{-1} for C mineralization rate, and mg (C or N) kg $soil^{-1}$ for pools.

Significant differences between untreated and detrital-pulse treated soils for each sampling date indicated by * ($p<0.05$), ** ($p<0.01$), and *** ($p<0.001$).

n.s. – not significant at $\alpha=0.05$.

† Sagebrush soils had significantly greater soluble organic C than cheatgrass or crested wheatgrass soils.

Table 3-6. Characteristics of soil organic matter fractions

SOM fraction	% of soil mass	organic C concentration	% of soil organic C	N concentration	% of soil N	C:N ratio
		mg C kg^{-1} fraction		mg N kg^{-1} fraction		
LF	1.6	329 (19)	3.8 (0.9)	18.8 (2.2)	2.4 (0.5)	18.2 (0.6)
MF	6.9	275 (31)	13.0 (1.6)	17.6 (2.1)	8.2 (0.9)	15.9 (0.1)
HF	93.7	8.6 (1.1)	53.3 (2.1)	1.27 (0.18)	87.7 (6.4)	6.9 (0.1)
Bulk soil		14.6 (0.6)		1.38 (0.06)		10.6 (0.4)

Table 3-7. Characteristics of microbial C and N dynamics from untreated and detrital-pulse soils in June

	Untreated	Detrital-pulse
N immobilization rate	2.3 ± 0.5	7.5 ± 1.5
Gross N mineralization rate	2.4 ± 0.3	7.9 ± 1.6
C mineralization rate	5.5 ± 0.5	7.1 ± 0.8
Microbial biomass C:N †	6.1 ± 0.5	4.8 ± 0.3
Substrate use efficiency ‡	62 ± 5 %	77 ± 4 %
Substrate C:N ratio §	8.4 ± 1.0	6.1 ± 0.9

Values are means (± s.e.) for the June sampling date; rates are expressed as mg (N or C) kg $soil^{-1}$ day^{-1}.

† Average of microbial C-flush to N-flush ratio.

‡ Calculated based on method of Schimel (1988), assuming balanced microbial growth and that only inorganic N is used for growth. SUE = G/(G+R) * 100%; where G = C assimilated into microbial biomass = gross N immobilization * microbial C:N; R = C respired as CO_2

§ Calculated from model described in Saetre and Stark (2005).

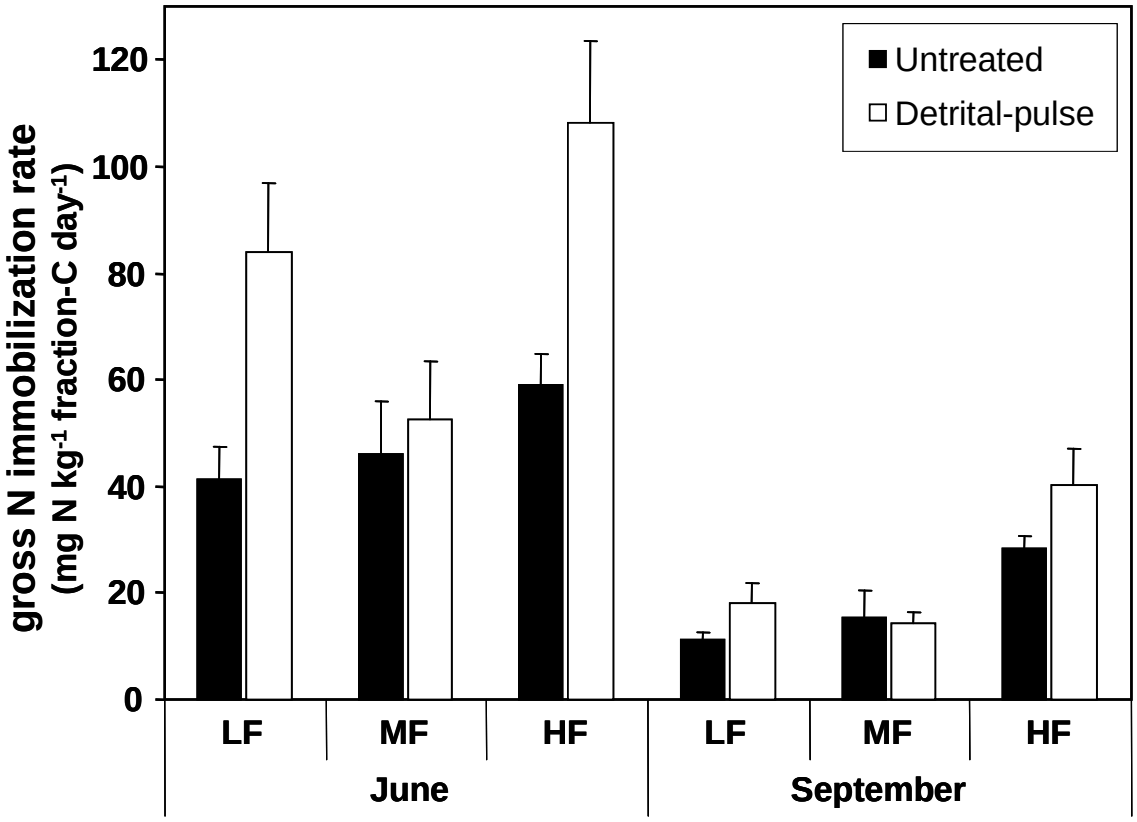

Figure 3-1. Immobilization of N into light (LF), medium (MF), and heavy (HF) organic matter fractions during June and September in untreated soils and soils receiving an *in situ* detrital pulse. Error bars represent 1 SE (n=4).

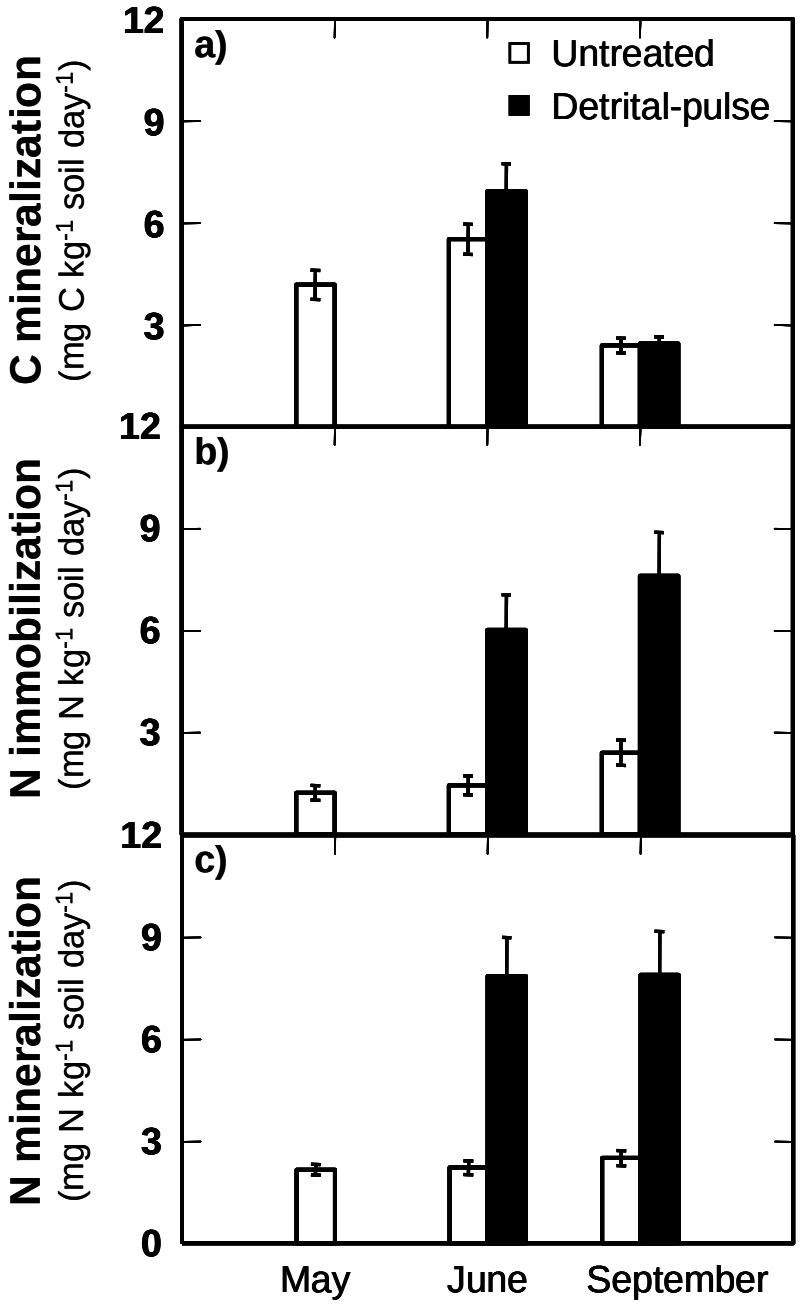

Figure 3-2. (a) C mineralization, (b) N immobilization, and (c) N mineralization rates from untreated (white) and detrital-pulse treated (black) soils in late-spring and summer 2003. Error bars represent 1 SE (n=12).

CHAPTER 4

CARBON FLOW FROM PLANT DETRITUS AND SOM TO SOIL MICROBES – LINKING C AND N CYCLING IN SEMIARID SOILS[1]

Abstract: In semiarid annual grass-dominated ecosystems, plant detritus is the dominant form of labile C input over a large portion of the year, but the contributions of plant detritus and soil organic matter to microbial substrate availability are unclear. We investigated the importance of current year plant detritus versus older soil organic matter as sources of substrates for microbial growth, and examined whether differential use of these substrates affected the balance between microbial N mineralization and immobilization processes. Since annual grass senescence commonly occurs with the onset of the summer dry-season, we hypothesized that microbial consumption of substrates derived from recently released plant detritus would increase significantly from summer to autumn, and that greater consumption of recent substrates, with wider C:N ratios, would be associated with greater N immobilization rates. We labeled a cohort of annual grass biomass *in situ* with $^{13}CO_2$ in intact mesocosms from soil beneath sagebrush and cheatgrass vegetation, and tracked the fate and turnover of ^{13}C into mineralizable and microbial biomass pools, and soil organic matter density fractions over 17 months. To determine whether microbial growth was N-limited, we compared gross rates of NH_4^+ and NO_3^- immobilization under stimulated (^{15}N-amended) and unstimulated conditions during short-term laboratory incubations on five sampling dates. We also examined seasonal differences in microbial activity associated with C-rich and N-rich microsites by

[1] Coauthored with Dr. John M. Stark

using ^{15}N to link N immobilization rates to organic matter density fractions.

Annual grass fine roots decomposed rapidly over 17 months (36% $month^{-1}$), based on the decrease in ^{13}C content over time, particularly between the first summer and autumn after plant senescence. Total soil organic ^{13}C decreased by 4% $month^{-1}$, and detrital-^{13}C was rapidly incorporated into both labile (microbial biomass and mineralizable C) and purportedly recalcitrant (heavy fraction, HF) soil organic matter pools. Nearly half of total ^{13}C in bulk soil (including roots) was contained within HF; however, microbial biomass-^{13}C could account for approximately 60% of HF-^{13}C, suggesting that a portion of HF organic matter is recent and relatively labile.

Soil ^{13}C mineralization rates increased significantly from summer to autumn, consistent with our hypothesis. However, this was driven by a large increase in total C mineralization rates, since the ^{13}C-enrichment of mineralizable C declined over time. In mid-summer, recently released detritus accounted for 12.7% of mineralized C. Faster rates of microbial ^{13}C versus total C turnover indicate that recent detritus was more labile than bulk soil organic matter during the first summer and autumn. Greater microbial consumption of recent detritus in autumn had no apparent effect on gross N cycling rates in bulk soils. NH_4^+ immobilization rates were rarely N-limited; instead, addition of $^{15}NH_4^+$ stimulated gross nitrification rates in summer and autumn, and only stimulated NH_4^+ immobilization rates in spring. Contrary to our hypothesis, these results suggest that microbial growth in these annual grass-dominated soils was C-limited for much of the year, when plants were not actively growing.

Soil organic matter fractions were important sinks for detrital ^{13}C and immobilized ^{15}N in this study. Differences in organic matter fraction N immobilization

rates between summer and autumn were subtle, and were only significant for the C-rich LF, but are consistent with greater microbial consumption of recent detritus in autumn. Rates of N immobilization were greatest for all organic matter fractions in spring and were positively correlated with soil C mineralization rates, indicating that organic matter fraction C was available as substrate fueling microbial growth. In addition, organic matter fraction N immobilization rates were correlated with organic matter fraction ^{13}C content during the first summer and autumn, and the rate of N immobilization per unit ^{13}C content increased from summer to autumn, such that the availability of recent detritus was an important driver for N immobilization in these organic matter fractions.

INTRODUCTION

The magnitude of carbon (C) cycling in terrestrial ecosystems - via plant net primary production and microbial organic matter decomposition - is strongly linked to soil nitrogen (N) dynamics. For example, changes in ecosystem C cycling driven by shifts in dominant vegetation type or in response to increasing atmospheric CO_2 appear to be constrained by the availability of soil N for uptake by plants or by soil microorganisms (McCulley et al. 2004, Gill et al. 2006, Reich et al. 2006). The supply of N made available during microbial decomposition of organic matter is regulated by the availability of labile C fueling microbial growth, the C:N stoichiometry of available substrates, and environmental factors such as soil temperature and moisture. An increase in the quantity of C inputs to soil should stimulate microbial N demand and reduce N available for plant uptake (Hart et al. 1994). Conversely, an increase in the quality of inputs (i.e. lower C:N ratios) should increase plant N availability, due to a decrease in

microbial demand for inorganic N per unit of C consumed (Chen and Stark 2000, Saetre and Stark 2005). However, plant detritus and soil organic matter are composed of a wide range of materials that vary in age, chemical structure, biological availability, and C:N stoichiometry. Greater understanding is needed of the sources of organic matter substrates consumed by microbes in order to better predict how ecosystem C storage and soil nutrient availability will respond to changes in dominant vegetation type or increasing CO_2 concentrations.

Shifts in dominant vegetation type have been reported to alter soil C and N availability through differences in the quantity and quality of plant detrital inputs (Vinton and Burke 1995, Evans et al. 2001, Carrera et al. 2003), particularly in semiarid ecosystems where rates of net primary production are low (Neary et al. 2003) and soil organic C and N pools are small (Schlesinger 1997). In semiarid rangelands of the Great Basin, sagebrush-dominated ecosystems are increasingly being invaded by the exotic annual cheatgrass (*Bromus tectorum*) (Bradley and Mustard 2005). Cheatgrass invasion and dominance is anticipated to result in a net decrease in ecosystem C storage, largely due to the loss of woody sagebrush biomass following wildfire (Bradley et al. 2006). However, recent work suggests that in the absence of wildfire, plant production and detrital inputs to soil may be greater in annual grass compared to sagebrush systems (Hooker et al. 2008). Many questions remain with regard to soil C and N dynamics in semiarid ecosystems, particularly with respect to the flow and fate of organic matter derived from plant detritus as it is decomposed by microbial biomass.

Large seasonal fluctuations in soil temperature and moisture, in addition to temporal differences in plant activity, may affect the relative availability of labile

substrates to soil microorganisms. In ecosystems with strong seasonality, rapid cycling of labile C and N and build-up of plant available nutrients may occur over periods when plants are not actively growing. For example, in a tropical semiarid savanna, the accumulation of soil inorganic N during the dry-season and depletion during the wet season could account for a large proportion of plant N uptake (Augustine and McNaughton 2004). In an alpine meadow ecosystem, labile N accumulated within microbial biomass from litter decomposition during autumn and winter, and was released as a pulse of plant available N during spring snow melt (Brooks et al. 1998, Schmidt and Lipson 2004, Schmidt et al. 2007). Since the release of microbial N and the accumulation of soil inorganic N are expected to result from a C-limitation to microbial growth (Hart et al. 1994, Chen and Stark 2000), these studies provide evidence for important seasonal shifts in N- versus C-limitations to microbial activity.

In semiarid annual grass-dominated ecosystems, plant senescence occurs with the onset of the summer dry-season (late May to early June; Stewart and Hull 1949, Harris 1967). This results in the cessation of plant rhizodeposition and the turnover of the entire plant biomass as detritus. Under these conditions, a large fraction of plant detrital inputs to soil are released as a seasonal pulse. These detrital inputs should result in a large increase in soil C availability, and fuel high rates of microbial growth and N immobilization. Instead, surface soils of annual grass-dominated ecosystems tend to accumulate large pools of NO_3^- during the summer (Jones and Woodmansee 1979, Booth et al. 2003), which suggests a C limitation to microbial N immobilization (Hart et al. 1994, Chen and Stark 2000), while soil NO_3^- concentrations return to low levels in autumn (Davidson et al. 1990, Schimel et al. 1989). Summertime microbial C limitation

in the face of large pools of recently released plant detritus may be due to abiotic restrictions on microbial activity in dry soils, such that there is a time-lag in microbial utilization of plant detritus until after soil moisture increases in autumn.

Our objective in this study was to investigate the importance of current year plant detritus versus older soil organic matter as sources of substrates for microbial growth. We examined whether microbial substrate use varied seasonally, and whether differential use of older versus more recent substrates affected the balance between microbial N mineralization and immobilization processes. In this study, we labeled a cohort of annual grass biomass *in situ* with $^{13}CO_2$ in intact mesocosms from soil beneath sagebrush and cheatgrass vegetation types, and tracked the fate and turnover of ^{13}C into mineralizable and microbial biomass C pools, and soil organic matter fractions over 17 months. To determine whether microbial growth was N-limited, we compared gross NH_4^+ and NO_3^- immobilization rates under stimulated (^{15}N-amended) and unstimulated conditions during short-term laboratory incubations. We also examined seasonal differences in the activity of microbes associated with C-rich and N-rich microsites by using ^{15}N to link N immobilization rates to organic matter density fractions. Since this semiarid ecosystem experiences a significant summer drought, we hypothesized that microbial consumption of substrates derived from recently deposited detritus would be greater in autumn compared to summer, as soil moisture increases. In addition, since the C:N ratio of plant detritus (26.6 ± 2.5 and 51.7 ± 4.5, for fine roots and senesced foliage, respectively) is greater than that of bulk soil organic matter (10.4 ± 0.4; Hooker et al. 2008), we hypothesized that greater microbial consumption of recent substrates would be associated with greater N immobilization rates. Thus, we expected that gross N immobilization

rates would increase from summer to autumn.

MATERIALS AND METHODS

Study site

This study was carried out in a Great Basin sagebrush ecosystem in Rush Valley (Tooele County), Utah (112˚ 28’ W, 40˚ 17’ N, elev. 1650 m). Vegetation at this site contains extensive, nearly monodominant stands of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young), and cheatgrass (*Bromus tectorum* L.). Cheatgrass-dominated areas established naturally in autumn 1992 after a summer wildfire consumed several large areas of sagebrush. Mean annual precipitation and temperature measured on-site over a 5-year period were 240 mm and 8.3 ˚C. Precipitation is distributed nearly evenly over the year, but soil water accumulation is restricted to the cooler autumn and winter months (November through March; see Table 4-1). Soils are derived from lacustrine and alluvial sediments of primarily limestone deposits, and classified as silt loam, very deep, well drained, file-silty, mixed, superactive, mesic Typic Calcixerolls (Trickler et al. 2000).

Mesocosm collection and ^{13}C plant biomass labeling

To track the fate of a cohort of plant detritus as it decomposed in the field, intact soil mesocosms were collected, cheatgrass plants were grown in the mesocosms with $^{13}CO_2$ in a greenhouse, then returned to the field, and harvested on five sampling dates over a 17-month period (Table 4-1). On each sampling date, intact soil cores were

collected from each mesocosm and incubated in the laboratory with ^{15}N to determine soil C and N cycling rates (see below).

The 24 intact mesocosms (22-cm diameter and 32-cm tall) from sagebrush (12) and cheatgrass (12) stands were collected from frozen soil in late-autumn 2003 by driving steel cylinders into the soil. The mesocosms were kept frozen until May 2004, when they were thawed, sown with 300 cheatgrass seeds, and placed in a greenhouse to allow seed germination and seedling establishment. Plants in mesocosms were labeled with $^{13}CO_2$ in a closed-system polycarbonate incubator (61-cm tall x 76-cm wide x 95-cm long), after the first true leaves were 2.5 cm long. Mesocosms were randomly assigned to three groups of 8, and each group was labeled for 4 hr every third day over 5 weeks. The $^{13}CO_2$ was generated by acidifying $NaH^{13}CO_3$ (>98 atom% ^{13}C; Isotec, St. Louis) with 5M H_3PO_4, and then the $^{13}CO_2$ was flushed into the incubator. Incubator CO_2 concentrations were monitored with a closed-path infrared gas analyzer (ADC LCA-2; Herts, U.K.), and were maintained within 50 ppm of greenhouse CO_2 concentrations (approximately 400 ppm) during the labeling periods. Approximately 25 mm of H_2O was added to each mesocosm during the first 3 weeks of labeling, and then they were allowed to dry. By the fifth week, cheatgrass plants had largely senesced and C uptake was not detectable. Two leaves from each mesocosm were collected and dried for isotopic analysis. Mesocosms were returned to the field and re-buried in their original locations in mid-June 2004. Mesocosms were covered with 1-cm mesh screens to inhibit herbivory of aboveground biomass and surface litter.

Mesocosms were harvested on 5 sampling dates (Table 4-1) during summer, autumn, and spring seasons in 2004 and 2005. In late November 2004 (after the second

sampling date), 300 seeds were added to each mesocosm to ensure germination the following year. Since autumn of year 2 (2005) was dry, we added 15-mm of supplemental water to the remaining mesocosms in late October, three weeks prior to the final sampling date.

Soil collection and laboratory incubation

On each sampling date, two mesocosms from each soil type were collected from the field and transported to the laboratory. Plant shoots and surface litter were carefully removed from the soil surface. Fifteen soil cores (3.5-cm diameter, 10-cm tall) were collected from the surface soil (0-10 cm) of each mesocosm, and separated into three groups to be incubated with $^{15}NH_4^+$, $^{15}NO_3^-$, or water additions (see below). Soils were incubated in canning jars at 25ºC in the laboratory with basetraps to collect CO_2 mineralized by soil microbes.

To examine soil N dynamics over time, five soil cores from each mesocosm were amended with six 1-mL injections of: 1) $(^{15}NH_4)_2SO_4$ (99 atom% ^{15}N), 2) $K^{15}NO_3$ (99 atom% ^{15}N), or 3) dilute K_2SO_4 (same ionic strength as ^{15}N solutions), using a side-port needle. Addition of $^{15}NH_4^+$ was used to measure gross N mineralization rates, $^{15}NO_3^-$ was used to measure gross nitrification rates, and dilute K_2SO_4 was used to measure unstimulated net N mineralization rates (see ^{15}N calculations below). Soil solution injections increased soil moisture by approximately 0.05 g H_2O g^{-1} soil. Additions of ^{15}N solutions were targeted to double extractable inorganic N pools. The $^{15}NH_4^+$ additions (2.3 mg ^{15}N / kg soil) increased extractable NH_4^+ pools by 132 ± 12% (standard error) over all sampling dates. Since soil NO_3^- concentrations are greater in summer than

autumn or spring, $^{15}NO_3^-$ additions (4.5 to 7.4 mg ^{15}N / kg) increased extractable NO_3^- pools by approximately 200% in autumn and spring, and by 90% in summer.

After a set of five cores from one mesocosm was injected with one type of N solution ($^{15}NH_4^+$, $^{15}NO_3^-$, or water), one of the cores was homogenized and a subsample (25-g dry weight) was extracted with 200 mL 2 M KCl (approximately 10 min. after the initial injection). The remaining four cores from each N-addition and mesocosm were placed in separate 1-L canning jars with basetraps (3.5 mL of 1 M NaOH), and incubated in the dark at 25 ± 1˚C. This process was repeated for all three N-additions and four mesocosms. Two cores from each N-addition and mesocosm were harvested at 24 h and at 48 h. During the harvest, basetraps were removed from jars, capped tightly and stored at 4˚C until analysis (see below). Soil from harvested cores was homogenized, and a subsample from each core was extracted with KCl as described above. The soil residue remaining after KCl extraction was dried at 70˚C and separated into organic matter density fractions (see below). Additional subsamples from incubated soils were collected to determine microbial biomass C and N using chloroform fumigation-extraction (Haubensak et al. 2002), using k_{EC} of 0.49 and k_{EN} of 0.62 (Herron et al. 2009). Briefly, paired subsamples (25-g dry weight) were either extracted with 200 mL 0.5 M K_2SO_4, or placed in 50-mL beakers in a glass vacuum desiccator containing 30-mL ethanol-free chloroform. Chloroform fumigation involved evacuation and flushing the desiccator three times, using a vacuum pump. After 72 h of fumigation, samples were extracted with 0.5 M K_2SO_4.

Laboratory analysis

Soil remaining in mesocosms after taking core samples within the 0-10 cm depth was passed through 2-mm (#10) and 1.18-mm (#16) mesh sieves to collect coarse fragments and root fragments, respectively. Roots were rinsed with 0.5 M HCl and sodium hexametaphosphate (5 g/L) solutions to remove carbonates and soil particles from root surfaces. Plant shoots, roots, and surface litter harvested from mesocosms were dried at 65°C for 72 hr, and ground with a Wiley mill to pass 60-mesh. Subsamples of plant shoots, roots, and surface litter were analyzed for C and N content and ^{13}C isotopic enrichment with a Europa 20/20 SL isotope ratio mass spectrometer (Sercon, Cheshire, U.K.). Mineral soils were dried at 65˚C, and ground with a roller mill, and subsamples were analyzed for C and N, and ^{13}C and ^{15}N enrichments after removal of inorganic C following the HCl fumigation method of Harris et al. (2001).

All soil extracts were shaken for 60 min. and stored in a cold room at 4ºC overnight to allow settling. Soil extracts were then filtered with pre-leached Whatman #4 filters, and the filtrates immediately frozen until analysis. Soluble organic C concentrations from fumigated and unfumigated K_2SO_4 extracts were analyzed with a Phoenix 8000 TOC analyzer (Teledyne-Tekmar, Mason, OH, USA). Concentrations of soil NH_4^+ and NO_3^- (2 M KCl), and total soluble N (0.5 M K_2SO_4) following persulfate oxidation (Cabrera and Beare 1993), were analyzed colorimetrically with a Lachat AE flow-injection autoanalyzer (Lachat Instruments, Milwaukee, WI, USA). Soil KCl extracts were diffused onto acidified filter paper disks for determination of ^{15}N atom

percent enrichment by mass spectrometry following the procedure described in Stark and Hart (1996).

Determination of C mineralization rate and CO_2-^{13}C enrichment

Carbon mineralization rates and ^{13}C-enrichment of mineralized C from soil incubations were determined from analysis of carbonate (CO_3^{2-}) in NaOH basetraps collected during each incubation interval. The CO_3^{2-} in aliquots of basetrap solution was converted to CO_2 by addition of excess 5 M H_3PO_4 in 22-mL gas vials capped with greased (Apiezon N) septa. The generated CO_2 gas was injected into a gas port placed between the combustion and reduction ovens of a Europa SL elemental analyzer and attached to an Europa 20/20 isotope ratio mass spectrometer (Sercon, Cheshire, U.S.). At least four basetrap blanks were incubated in jars without soil per incubation interval and sampling date, in addition to non-incubated solution blanks. The relationship between C content of basetraps and C content of injected CO_2 was established empirically, where known amounts of pure CO_2 were added to incubation jars containing basetraps, and the C content and isotope ratio was determined as above. Previous work indicates that C content derived from mass spectrometer data was accurate in comparison with the same analysis by gas chromatography (TCD detector, Varian Instruments, Walnut Creek, CA). After blank-correction, the relative standard deviation of ^{13}C isotope ratios (as ^{13}C atom percent) from all calibration samples was less than 0.05 %. The ^{13}C-enrichment of mineralized C is reported as ^{13}C atom percent excess, based on the ^{13}C natural abundance of soil organic C (1.084 atom% ^{13}C).

^{13}C-enrichment of microbial biomass C

The ^{13}C-enrichment of 0.5 M K_2SO_4 extractable organic C was determined for both chloroform-fumigated and unfumigated K_2SO_4 extracts by alkaline persulfate oxidation, liberation of trapped CO_3^{2-} as CO_2, and injection into an isotope ratio mass spectrometer. Briefly, 10 mL of K_2SO_4 extract were added to 60-mL glass vials, and then pre-treated with 5 M H_3PO_4 (to pH 5) and sparged with N_2 for 5 min to remove inorganic C. Next, 10 mL of persulfate digestion reagent (following Doyle et al. 2004) was added to each vial. Vials were capped with phenolic lids containing PTFE-silicone septa (73804, and 73818A-24, Kimble, Vineland, NJ). Samples were inverted and digested in an oven at 90°C for 12 hr. After the digestion tubes had cooled, 5 mL of 5 M H_3PO_4 was added to liberate CO_2, and 5 mL of headspace gas was injected into a gas-port attached to the mass spectrometer. The ^{13}C atom percent of CO_2 was corrected for C in solution blanks between dissolved and aqueous CO_2. Microbial biomass ^{13}C atom percent was calculated as:

$$= \frac{\left(F_C \times F_{^{13}C} - U_C \times U_{^{13}C}\right)}{\left(F_C - U_C\right)} \text{ x } 100 \qquad (1)$$

where F_C and U_C are total organic C contents (mg C / kg soil) for fumigated and unfumigated soil extracts, respectively, and F_{13C} and U_{13C} are ^{13}C atom fraction. All reported data and calculations were based on ^{13}C atom% excess; the ^{13}C natural abundance of microbial biomass was determined from un-labeled soils (-22.9 ± 0.5 ‰ and -25.4 ± 0.5 ‰ for cheatgrass and sagebrush soils, respectively).

Calculation of gross N cycling rates

Gross N mineralization and nitrification rates were calculated from isotope dilution equations (see Stark 2000). Gross rates of microbial NH_4^+ and NO_3^- consumption were calculated as:

Gross consumption = Gross production – net production (2)

Since the addition of ^{15}N to soil inorganic N pools may stimulate microbial N consumption rates if N is limiting (Davidson et al. 1991) but gross production rates should be unaffected, we calculated consumption rates under N-stimulated and unstimulated conditions. Unstimulated consumption rates were based on net production rates from cores that received only dilute K_2SO_4. Dilute K_2SO_4 was used instead of deionized water to account for potential confounding effects of solution ionic strength on net rates. Stimulated consumption was based on net production in ^{15}N-amended cores during the incubation.

The addition of $^{15}NH_4^+$ may stimulate either microbial NH_4^+ immobilization or autotrophic nitrification rates, or both. Stimulated nitrification rates were calculated based on the appearance of added $^{15}NH_4^+$ in the $^{15}NO_3^-$ pool over the course of the incubation:

$$M_{AB} = \frac{P_{Bt} \cdot (E_{Bt} - E_{B0})}{(E_{A0} + E_{At})/2} \Big/ t \qquad (3)$$

where M_{AB} is the nitrification rate from source pool A (NH_4^+) to sink pool B (NO_3^-), P is the NO_3^- pool size, E is the ^{15}N atom percent excess of source and sink pools at time-0 and time-t, and t is time in days (following Davidson et al. 1991). Gross NH_4^+

immobilization was calculated as:

Gross NH_4^+ immobilization = Gross NH_4^+ consumption – Gross nitrification (4)

and was calculated for both stimulated and unstimulated conditions.

Separation of soil organic matter density fractions

Soil residues, obtained following KCl extraction of ^{15}N amended soils, were dried at 70˚C, sieved (<1 mm) to remove intact roots, and then separated into three density fractions using a procedure modified from Magid et al. (2002). Approximately 12 g of dry soil residue were placed in 50-mL centrifuge tubes with 30 mL of sodium hexametaphosphate (HMP, 5 g/L) in 1.5 M KCl solution ($\rho \sim 1.08$ g cm^{-3}), shaken for 30 min., and then centrifuged at 2100 rpm (900 x g). We used 1.5 M KCl in an effort to reduce the potential for osmotic up-shock of soil microbes that might result in release of cytoplasmic ^{15}N to the solution (Kieft et al. 1987). The floating light fraction (LF, $\rho \leq 1.0$ g cm^{-3}) material was collected by decanting the supernatant onto a Falcon bottle-top filter unit (part no. 357105, Becton-Dickinson, Franklin Lakes, NJ, USA) holding a Millipore 0.45 μm membrane (HAWP 047, Billerica, MA). The pellet was re-suspended with fresh solution, and the procedure repeated twice more. Medium fraction organic matter (MF, $1.0 < \rho \leq 1.70$ g cm^{-3}) was then collected by re-suspending the pellet with 30 mL of sodium polytungstate ($\rho = 1.70$ g cm^{-3}; Sometu, Van Nuys, CA, USA), and the same process repeated twice using a second Falcon filter unit and membrane. The remaining pellet contained the heavy fraction organic matter (HF, $\rho > 1.70$ g cm^{-3}). Residual sodium polytungstate was removed from the heavy fraction by re-suspending the pellet in deionized water, and shaking, centrifuging and decanting two more times.

Light fraction and medium fraction materials were carefully scraped off the membranes. All organic matter fractions were dried at 70ºC for 48 h, and weighed, and then ground with a mortar and pestle. Subsamples of LF and MF were wrapped in 8x5 mm tin capsules, for C and N elemental and ^{13}C and ^{15}N isotopic analysis with a Europa 20/20 SL isotope ratio mass spectrometer (Sercon, Cheshire, U.K.). Heavy fraction C, N, ^{13}C and ^{15}N analyses were performed after removal of inorganic C using the HCl fumigation method of Harris et al. (2001).

Calculations and statistical analysis

Rates of N immobilization into soil organic matter density fractions (LF, MF, and HF) were calculated based on the appearance of ^{15}N in the organic matter fractions, after correcting for initial (T0) ^{15}N content and declining ^{15}N enrichment of source pools, following Davidson et al. (1991), as in equation 3 above, where M_{AB} is the N immobilization rate from source pool A to organic matter fraction B. Because a large quantity of added $^{15}NH_4^+$ was nitrified during laboratory incubations, but only small quantities of added $^{15}NO_3^-$ were remineralized (see Table 4-4), we first calculated rates of NO_3^- immobilization as outlined above, and then used these rates to account for ^{15}N content that may have been due to NO_3^- rather than NH_4^+ immobilization in $^{15}NH_4^+$ amended soils. We assumed that rates of NO_3^- immobilization among organic matter fractions were not affected by larger NH_4^+ pools in $^{15}NH_4^+$ amended soils. The quantity of organic matter fraction ^{15}N attributed to $^{15}NO_3^-$ immobilization was accounted for by rearranging equation 3 and solving for ^{15}N content of the sink (i.e. the numerator term), using the rate of $^{15}NO_3^-$ immobilization and the NO_3^--^{15}N enrichment (in $^{15}NH_4^+$ amended

soils). Rates of NH_4^+ immobilization were then calculated using equation 3, using the corrected ^{15}N content. Results are expressed as N immobilization rate per unit organic matter fraction C.

Microbial turnover rates were calculated from total organic C, ^{13}C, and N by dividing total C-, ^{13}C-, and N mineralization rates by the respective microbial biomass pool, expressed in units of mg mineralized mg^{-1} biomass day^{-1}.

Comparisons of soil C and N cycling rates among soil types (cheatgrass and sagebrush-dominated soils) and sampling dates were analyzed using the SAS mixed procedure (SAS version 9.0, Cary, NC). Soil type and sampling date were fixed factors, and mesocosms within soil types were considered random effects. The error-covariance matrix was modeled with several different structures, and the best model was selected based on AICC and BIC information criteria for each variable. Additional fixed factors were added to examine the effect of ^{15}N addition on gross NH_4^+ immobilization and nitrification rates, and to compare N immobilization rates among light-, medium-, and heavy fractions. Variables were transformed when necessary to comply with model assumptions; data were most commonly natural log transformed. Statistical comparisons were considered significant at $\alpha = 0.05$.

RESULTS

There was little difference in microbial C and N cycling between soils collected beneath sagebrush and cheatgrass vegetation. The one exception was that cheatgrass soils generally had faster rates of gross NO_3^- production and consumption than sagebrush soils ($p<0.01$ and $p<0.07$, respectively). Because of few soil type differences, we focus

on the seasonal dynamics of microbial C and N cycling during the decomposition of the ^{13}C-labeled cohort of plant detritus.

Distribution of ^{13}C-labeled plant detritus

On the first sampling date, mesocosms contained 2.83 ± 0.24 mg ^{13}C excess kg^{-1} soil within the 0-10 cm depth (Table 4-2), which accounted for approximately 70% of total ^{13}C in mesocosms. The ^{13}C content within the surface soil (0-10 cm) declined by 45% over 17 months in the field. Fine roots and microbial biomass were the dominant sinks for ^{13}C in soils on the first sampling date (Table 4-2). Fine root ^{13}C content declined rapidly between the first (summer) and second (autumn) sampling dates (Figure 4-1). This decline was largely due to lower fine root mass, since the ^{13}C-enrichment of fine roots did not decline appreciably during this period (data not shown). However, the decline in root ^{13}C could not be directly linked to an increase in ^{13}C in either microbial biomass or soil organic matter density fractions (Figure 4-2). Heavy fraction organic matter was the dominant sink for ^{13}C among organic matter fractions, but the ^{13}C-enrichment of the LF was greater than both HF and MF materials (data not shown).

Seasonal patterns of soil C and N dynamics

Both the rate of C mineralization during laboratory incubations and the quantity of microbial biomass were greater in moist autumn and spring soils compared to dry summer soils ($p<0.001$ for both). The ^{13}C-enrichment of mineralized C declined from summer to spring, and remained relatively constant thereafter (Figure 4-3). Consequently, the quantity of recent (^{13}C-labeled) detritus mineralized by soil microbes

increased from summer to autumn during both years, but was lower in spring than the preceding autumn.

Microbial biomass averaged 550 mg C / kg soil in dry summer soils, and increased to approximately 890 mg C/kg soil in moist autumn and spring soils ($p<0.002$; Figure 4-4). Microbial biomass ^{13}C-enrichment declined significantly from summer to autumn during both years ($p<0.0001$). The ^{13}C-content of microbial biomass declined by approximately 50% (from 0.8 to 0.4 mg ^{13}C/kg soil) over 17 months.

The C:N ratios of foliage and fine roots from recently senesced cheatgrass plants averaged 49.0 and 32.5, respectively, across both soil types. The C:N ratio of microbial biomass was approximately 8.1; these values did not differ significantly between soil types ($p=0.62$). Soil organic matter density fractions had C:N ratios of 15.6 (LF), 13.8 (MF), and 8.5 (HF), averaged across all soils and sampling dates.

Gross rates of N cycling during laboratory incubations varied significantly among sampling dates, but mainly due to faster rates of NH_4^+ cycling in spring compared to summer or autumn (Table 4-3). Rates of NO_3^- cycling did not significantly differ among sampling dates, but nitrification ranged from 32% of N mineralization in spring to 95% in autumn, and NO_3^- consumption accounted for approximately 40% of total N immobilization in these soils.

Overall, both NH_4^+ consumption and NH_4^+ immobilization rates covaried with N mineralization rates (slope = 0.72, $r^2 = 0.72$, $p<0.0001$, and slope = 0.64, $r^2 = 0.73$, $p<0.0001$, respectively), suggesting that NH_4^+ availability constrained rates of microbial N immobilization (Figure 4-5). Production and consumption of NO_3^- were also correlated (slope = 0.85, $r^2 = 0.60$, $p<0.0001$); however, nitrification was not correlated

with N mineralization ($r^2 = 0.01$, $p=0.20$). Addition of ^{15}N had a significant effect on the fate of NH_4^+ consumed by microbes (Table 4-3; stimulated versus unstimulated rates), but the results varied seasonally. NH_4^+ immobilization was stimulated only in spring (+53%, $p<0.013$), while nitrification was stimulated only in summer (+160%) and autumn (+70%, $p<0.0001$) (Figure 4-6). Addition of $^{15}NO_3^-$ had no significant effect on NO_3^- consumption rates ($p=0.90$).

Soil microbial C and N turnover

Microbial turnover rates of ^{13}C, C and N, calculated as the mineralization rate divided by microbial biomass, varied significantly among sampling dates ($p<0.0001$ for all; Figure 4-7). Microbial ^{13}C turnover ranged from approximately 2.4 to 3.2% d^{-1} the first year of decomposition in the field. This rate was significantly faster ($p<0.004$) than total C turnover during the first summer and autumn sampling dates (1.3 to 2.1% d^{-1}) (Figure 4-7a). In spring, total C turnover was significantly greater than in summer or autumn, and greater than ^{13}C turnover ($p<0.001$). Microbial biomass N turnover rates were most rapid in both summer and spring (3.6% d^{-1}) and slower in autumn (1.7% d^{-1}; Figure 4-7b).

N immobilization associated with organic matter fractions

Density fractionation of KCl-extracted residues resulted in recovery of 94% of soil organic C and N, and 85% of ^{13}C content. Approximately 90% of the ^{15}N added was recovered in soil organic matter fractions and inorganic N pools (Table 4-4); the remainder may have been lost during the density-separation procedure. Light and

medium particulate organic matter fractions accounted for 7.7 and 13.2% of soil C, and 4.8 and 9.2% of soil N, respectively, while the remainder occurred in the mineral-associated heavy fraction, which accounted for over 98% of soil mass. All three soil organic matter density fractions immobilized significant quantities of ^{15}N during short-term laboratory incubations, and N immobilization rates differed with season (Figure 4-8). Across all sampling dates, LF and HF N immobilization rates, expressed per unit organic C, were both greater than the MF ($p<0.001$). Nitrogen immobilization rates in organic matter fractions differed significantly by sampling date ($p<0.005$ for all; Figure 4-8), and were greater for NH_4^+ than NO_3^- ($p<0.001$ for all). Total N immobilization ($NH_4^+ + NO_3^-$) into LF increased significantly from summer to autumn in both years ($p<0.05$ for both organic matter fractions), and was greatest in spring. A similar pattern was observed for HF, however, the increase in N immobilization rates from summer to autumn was only significant during the second year of the study ($p=0.21$ for first year, and $p<0.05$ for the second year), and for MF only spring was significantly greater than summer or autumn.

DISCUSSION

Dynamics of soil C-flow

Our results address two important components of soil C dynamics in semiarid ecosystems: estimation of *in situ* rates of annual grass decomposition, and the distribution of detrital C among soil organic matter pools as this material decomposes. While most decomposition studies utilize litter bags, where decomposition rates may not mimic

natural decomposition processes, we calculated decay rates of detritus based on the decrease in ^{13}C content of fine roots and total soil (bulk) organic C pools over 17 months of incubation in the field (Table 4-2). Fine roots exhibited rapid decomposition (36.2 % $month^{-1}$) compared to total soil organic ^{13}C (4.0 % $month^{-1}$), illustrating the rapid decomposition of annual grass fine root detritus, particularly between the first summer and autumn after plant senescence (Figure 4-2). The initial rapid loss of fine root ^{13}C followed by a slower decrease in ^{13}C over time may be indicative of loss of soluble components of detritus during early stages of decomposition, and later slower degradation of plant polymers. Bird and Torn (2006) used a double exponential decay model to describe decomposition of added ^{13}C-labeled detritus in intact soil mesocosms, and reported rapid turnover of a labile C pool (from 8 to 57% $month^{-1}$), and slower turnover of a larger, more recalcitrant C pool (0.25 to 2% $month^{-1}$). Using the same model with our root ^{13}C data, we predict a large labile C pool with rapid turnover (over 50% $month^{-1}$) and smaller more recalcitrant C pool with slower turnover (8.8% $month^{-1}$). Conceptually, a double exponential model may be justified to describe *in situ* decomposition. Using litter bags, Parker et al. (1984) calculated rapid decay constants for root and leaf litter mass loss (13 to 22% $month^{-1}$) of a Chihuahuan desert annual forb during the early stages (100 days) of decomposition, while other studies reported much slower decay rates for perennial grass decomposition from other semiarid ecosystems over long time-periods (rate constants ranging from 1.6 to 3.7 % $month^{-1}$) (Harrison 2003, Gill and Burke 2002, Moretto and Distel 2003, Semmartin et al. 2004, Giese et al. 2009). However, more intense sampling over time is needed in order to obtain greater confidence in parameter estimates. It is currently unclear to what extent the range in

reported values for decomposition rate constants from semiarid ecosystems results from methodological differences (e.g. duration of experiment, litter bag versus ^{13}C *in situ* labeling) rather than from differences in the structure and chemical composition of plant detritus.

Carbon derived from annual grass detritus was rapidly incorporated into both labile (i.e. microbial biomass and mineralizable C) and purportedly recalcitrant (i.e. heavy fraction) soil organic matter pools. The initial recovery of detrital-^{13}C in labile pools was likely due to microbial consumption of plant rhizodeposits released during the growing season (Kuzyakov and Domanski 2000, Butler et al. 2004), since microbial biomass can contain 10 to 25% of C derived from rhizodeposits by the end of the growing season (Yevdokimov et al. 2006, Wichern et al. 2007). After 17 months of decomposition in the field, nearly 50% of the annual grass detrital-^{13}C in mesocosms was lost (mineralized), approximately 33% was retained as non-microbial soil organic matter, and 14% was in microbial biomass (Figure 4-1).

The large quantity of ^{13}C recovered in HF relative to the LF (Figure 4-2) is somewhat surprising. Heavy fraction organic matter is considered to represent a pool dominated by stabilized mineral-associated organic matter derived from microbial C sources, while the light fraction organic matter represents a pool dominated by recent, relatively undecomposed organic matter (Kiem and Kogel-Knaber 2003, Gregorich et al. 2006, Sollins et al. 2006, Grandy et al. 2007). However, recent work suggests that the HF may also contain C that is both recent and relatively labile (Chotte et al. 1998, Swanston et al. 2002, 2005, Crow et al. 2006, Hooker and Stark 2008). Our results indicate that across all sampling dates, microbial biomass ^{13}C could account for

approximately 45% of ^{13}C content in HF, but only 7% of total organic C in HF. Nonetheless, even assuming that all of the microbial biomass ^{13}C was contained within the HF, the non-microbial HF would still contain more ^{13}C on all sampling dates than either of the two other organic matter fractions combined. These results provide additional evidence that HF organic matter is not as recalcitrant as formerly thought, and support previous work suggesting that much of HF organic matter is microbial in origin.

Seasonal variation in soil C dynamics

We observed consistent seasonal differences in the size of microbial biomass and rates of C mineralization in this study. Both microbial biomass C pools and C mineralization rates were greater in soils from moist autumn and spring sampling dates compared to those collected in summer (Figures 4-3a and 4-4a), indicating a seasonal increase in soil C availability in autumn and spring. Our initial hypothesis was that microbial consumption of substrates from recently deposited detritus would increase from summer to autumn, since low soil moisture during the summer dry-season was expected to inhibit microbial colonization of recently released plant detritus. Soil ^{13}C mineralization rates were significantly greater in autumn compared to summer (Figure 4-3c), which is consistent with our hypothesis. However, this was driven by the large increase in total C mineralization rates, since the ^{13}C-enrichment of mineralized C in autumn was lower than that from soils in summer (Figure 4-3b). The decline in ^{13}C-enrichment of mineralized C and microbial biomass over time suggests that the relative contribution of recent detritus to soil C availability decreased from summer to autumn, which does not support our hypothesis. Given the rapid decomposition of root biomass

and the distribution of detrital C throughout soil organic matter pools, we find no clear evidence of a time-lag in microbial colonization of recently released plant detritus.

These results lead to important questions regarding the source and turnover of microbial substrates in semiarid soils: What is the relative contribution of recent detrital C as substrate to soil microbes? How labile is detrital C compared to bulk organic C? We calculated the relative contribution of detrital C to microbially available C based on the ^{13}C-enrichment of microbial biomass and mineralized C (from data shown in Figures 4-3b and 4-4b), and the assumption that plant detritus had the same initial ^{13}C-enrichment as foliage at the end of the labeling period (1.83 ^{13}C atom% excess). In mid-summer, approximately 6 weeks after annual grass senescence, 12.7% of mineralized C and 8.9% of microbial biomass C was derived from recent detritus; in autumn, detrital C contributions to microbially available C had declined by roughly 50% (to 6.9% and 4.9%, respectively). Further reduction in detrital C contribution to mineralized C in spring is attributable to dilution with unlabeled C added from plant rhizodeposits. These results are similar to studies of ^{13}C partitioning of rhizodeposition during plant growth (Yevdokimov et al. 2006, Wichern et al. 2007), and suggest a gradual decline in detrital-C availability after plant senescence. Moreover, these results provide a sense of the importance of substrates derived from recent plant detritus relative to older, more highly decomposed mineral-associated organic matter, since recent inputs of detrital C accounted for only 0.9% of soil bulk organic C. Our data on microbial C and ^{13}C turnover rates (Figure 4-7a) also showed that substrates derived from recent detritus were more labile than bulk organic C during the summer and autumn after plant senescence.

Seasonal variation in soil N dynamics

The increase in microbial consumption of substrates derived from recent detritus (as ^{13}C mineralization rate) from summer to autumn did not translate into greater gross N immobilization rates in autumn in bulk soils (Table 4-3). Heterotrophic NH_4^+ immobilization rates in bulk soils were rarely N-limited. Instead, $^{15}NH_4^+$ addition significantly stimulated gross nitrification rates in summer and autumn (Figure 4-6). These results suggest that, contrary to our hypothesis, microbial activity in these annual grass-dominated soils was C-limited, and that the substrates released from plant detritus and soil organic matter between summer and autumn had narrow C:N ratios. Since the contribution of microbial substrates from recent detritus was approximately 12.7% in summer and 6.9% in autumn, microbial consumption of these substrates may have been too slow to have a statistically significant effect on gross N cycling rates in bulk soils. Nonetheless, rapid decomposition of fine root detritus between summer and autumn did not result in N-limitations to microbial growth in this annual grass-dominated soil.

Interestingly, when annual grasses were actively growing in spring, gross N cycling rates were significantly faster than rates in either summer or autumn, and NH_4^+ immobilization rates were significantly stimulated by $^{15}NH_4^+$ addition, indicating microbial growth was N-limited. Faster rates of microbial C and N cycling in spring were likely due to greater availability of labile substrates derived from plant rhizodeposits and fine root turnover (Herman et al. 2006, Yevdokimov et al. 2006, Hawkes et al. 2007), as evidenced by rapid rates of both microbial C and N turnover (Figure 4-7).

Sinks for immobilized N

All three soil organic matter fractions were significant sinks for immobilized N on all sampling dates. In contrast to N immobilization rates from bulk soils, N immobilization rates associated with C-rich light fraction organic matter increased significantly from summer to autumn (Figure 4-8); this is consistent with greater microbial consumption of recently released detritus in autumn. However, since this organic matter fraction constitutes only a small proportion of bulk soil organic matter, seasonal variations in microbial activity associated with LF may not necessarily be detectable by analysis of gross N cycling rates in bulk soils. Differences in N immobilization into the heavier MF and HF between summer and autumn were more subtle, and were not consistently significant during the two years measurements were made (Figure 4-8); thus, it is difficult to conclude whether greater microbial consumption of recent detritus in autumn had any meaningful impact on N immobilization rates in these N-rich organic matter fractions.

Previous studies have found the LF to be an important sink for immobilized N (Recous et al. 1999, Whalen et al. 2001, Compton and Boone 2002, Hooker and Stark 2008), and recent work suggests that at least a portion of HF C is recent and relatively labile (Swanston et al. 2002, 2005), and that the HF is also an important N sink (Hooker and Stark 2008). N immobilization rates associated with organic matter fractions were highest in spring, consistent with rapid rates of C and ^{13}C mineralization and microbial turnover. We also found that organic matter fraction N immobilization rates were positively correlated with C mineralization rates ($r^2 > 0.50$ for all fractions) across

sampling dates (data not shown), consistent with the observed seasonal increase in soil C availability, and suggesting that the C associated with these organic matter fractions was available to fuel microbial growth. Interestingly, we found that organic matter fraction N immobilization rates increased with organic matter fraction ^{13}C content during the first summer and autumn sampling dates (Figure 4-9), suggesting that recently released detrital C was an important driver for N immobilization in these fractions.

Conclusion

In situ plant ^{13}C labeling is a powerful approach that can be used to quantify decomposition rates in intact soils, and to track the fate and activity of detrital-C during decomposition. Our results revealed rapid decomposition of annual grass detritus over 17 months in the field, and rapid incorporation of detrital-^{13}C into both labile and purportedly recalcitrant soil organic matter pools. Microbial consumption of recent detritus increased between summer and autumn; however, since the relative contribution of recent detritus to total microbial C availability declined by 50% during the same time period, we find no clear evidence to support our hypothesis of a time-lag in microbial colonization of recent detritus between summer and autumn.

We observed few clear linkages between microbial consumption of recently released plant detritus and bulk soil N dynamics. Greater microbial consumption of recent detritus in autumn versus summer had no apparent effect on bulk soil gross N immobilization rates, and did not result in N-limitations to microbial growth in this annual grass-dominated soil. In contrast, N immobilization rates associated with soil organic matter density fractions revealed subtle seasonal patterns, especially in

particulate organic matter (LF), suggesting that the N dynamics of C-rich organic matter fractions may not necessarily be reveled by analysis of bulk soils. The heavier, mineral-associated organic matter fractions (MF and HF) were also important sinks for immobilized N in this study, but differences in N immobilization rates were not significant between summer and autumn. Interestingly, while nearly half of ^{13}C in bulk soil was contained within mineral-associated organic matter (HF), much of this recently derived C could be accounted for as microbial biomass ^{13}C, suggesting that at least a portion of HF organic matter is recent and relatively labile.

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Table 4-1. Soil and environmental conditions during study

Sampling Date	Season	Air T	Soil T at 10-cm	14-d precip.*	Soil		
					Moisture	NH_4^+-N	NO_3^--N
		------ (ºC) ------		(mm)	(g / g)	(mg N / kg soil)	
8/04	Summer	23.5	25.6	3.0	0.07	1.0	7.6
11/04	Autumn	7.5	6.6	32.6	0.21	1.3	1.4
5/05	Spring	10.3	9.2	53.6	0.25	2.2	0.8
9/05	Summer	22.0	22.5	<1.0	0.04	1.9	6.2
11/05	Autumn	-0.6	2.8	15.0	0.18	2.0	5.0

* Cumulative 14-day antecedent precipitation, measured on site.

Table 4-2. Distribution and decay rates of ^{13}C in soil organic matter pools

Sampling Date	Fine root C	^{13}C distribution		
		Microbial biomass	Roots + Soil (0-10 cm) †	Non-microbial SOM §
		(mg ^{13}C excess / kg soil)		
8/04	1.32	0.84	2.83	0.67
	(0.17)	(0.10)	(0.24)	(0.05)
11/04	0.35	0.70	2.17	1.13
	(0.09)	(0.06)	(0.14)	(0.13)
5/05	0.18	0.62	1.93	1.13
	(0.10)	(0.04)	(0.34)	(0.32)
9/05	0.07	0.39	1.69	1.23
	(0.03)	(0.02)	(0.23)	(0.08)
11/05	0.11	0.41	1.48	0.94
	(0.05)	(0.05)	(0.22)	(0.10)
		(% month^{-1})		
Mean ^{13}C decay constant ‡	23.3 ± 7.2	4.7 ± 0.8	4.0 ± 0.6	n.a.

Data shown are averages of four mesocosms per sampling date (standard error in parentheses).

† Sum of root and mineral soil ^{13}C content.

§ Total soil ^{13}C minus fine root and microbial biomass ^{13}C content

‡ Decay rates were calculated by fitting $Y_t = Y_1 \cdot e^{-kt}$, where Y = where ^{13}C content of pool on first (Y_1) and subsequent (Y_t) sampling dates, t = cumulative number of days mesocosms were in the field, and solving for k using the nonlinear regression component of SYSTAT. Decay rates are expressed as percent per month (% month^{-1}).

n.a. Not applicable.

Table 4-3. Seasonal patterns of gross N cycling rates during laboratory incubation of intact soil cores

	2 Aug. 2004 Summer	8 Nov. 2004 Autumn	5 May 2005 Spring	5 Sept. 2005 Summer	19 Nov. 2005 Autumn	P(Date)
	---------- mg N kg^{-1} soil day^{-1} ----------					
N mineralization	2.27 (0.33) b	1.57 (0.29) b	4.07 (0.48) a	1.81 (0.21) b	1.92 (0.22) b	<0.001
NH_4^+ consumption	2.25 (0.32) b	2.09 (0.25) b	3.65 (0.38) a	2.03 (0.17) b	2.46 (0.30) b	0.01
- *stimulated* -	3.53 (0.34) *	2.85 (0.31) *	4.71 (0.51) *	3.79 (0.28) *	4.00 (0.27) *	
Nitrification	1.17 (0.27)	1.40 (0.23)	1.32 (0.14)	1.07 (0.17)	1.89 (0.35)	0.17 ns
- *stimulated* -	2.43 (0.17) *	2.15 (0.35) *	1.33 (0.23)	2.67 (0.17) *	3.09 (0.27) *	
NH_4^+ immobilization	1.08 (0.21) b	0.98 (0.19) b	2.33 (0.35) a	0.97 (0.18) b	0.96 (0.23) b	0.02
- *stimulated* -	1.13 (0.25)	0.70 (0.14)	3.37 (0.41) *	1.11 (0.19)	0.96 (0.13)	
NO_3^- consumption	1.07 (0.24)	0.60 (0.16)	1.09 (0.13)	0.64 (0.25)	1.00 (0.37)	0.24 ns
N immobilization	2.42 (0.29) ab	1.58 (0.21) b	3.42 (0.38) a	1.61 (0.26) b	2.00 (0.35) b	0.04

Data shown are averages of four mesocosms per sampling date (standard error in parentheses), and sampling date main effect from analysis of variance models.

There was little evidence of significant differences in N cycling rates among soil types, except that NO_3^- production and consumption rates were slightly faster in cheatgrass versus sagebrush soils ($p<0.01$ and <0.07, respectively).

* Gross rate was significantly stimulated by addition of $^{15}NH_4^+$; $^{15}NO_3^-$ addition had no significant effect on NO_3^- consumption rates.

Lowercase letters indicate significant differences among sampling dates.

Table 4-4. Recovery of ^{15}N-labeled NH_4^+ and NO_3^- in inorganic N and soil organic matter fractions at the end of laboratory incubations.

	---------- % of initial ^{15}N added to core ----------					
Sampling Date	NH_4^+	NO_3^-	LF	MF	HF	Total
+ $^{15}NH_4^+$						
8/04	5.2	79.8	0.5	0.4	5.6	91.5
11/04	14.3	69.4	0.9	0.7	9.2	94.5
5/05	17.6	25.5	1.8	2.4	20.4	67.7
9/05	24.6	56.7	0.4	0.3	5.1	87.1
11/05	18.0	68.1	0.9	0.6	8.3	96.0
Average	*16.0*	*59.9*	*0.9*	*0.9*	*9.7*	*87.4*
+ $^{15}NO_3^-$						
8/04	0.1	95.4	0.1	0.1	1.1	96.8
11/04	0.1	95.6	0.2	0.1	2.5	98.6
5/05	6.0	39.3	1.0	1.9	16.4	63.6
9/05	0.1	100.1	0.1	0.1	1.1	101.5
11/05	0.2	99.2	0.2	0.1	1.7	101.4
Average	*1.3*	*85.7*	*0.3*	*0.4*	*4.6*	*92.4*

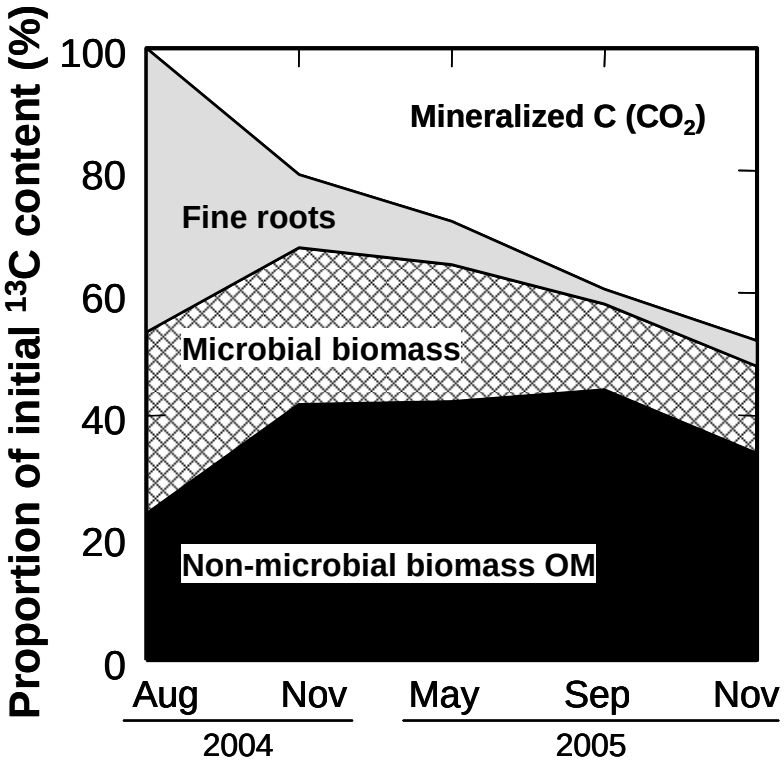

Figure 4-1. Change in relative distribution of ^{13}C (excess) among fine root, microbial biomass, and non-microbial biomass soil organic matter pools during 17 months of field incubation. Values are expressed relative to the first sampling date.

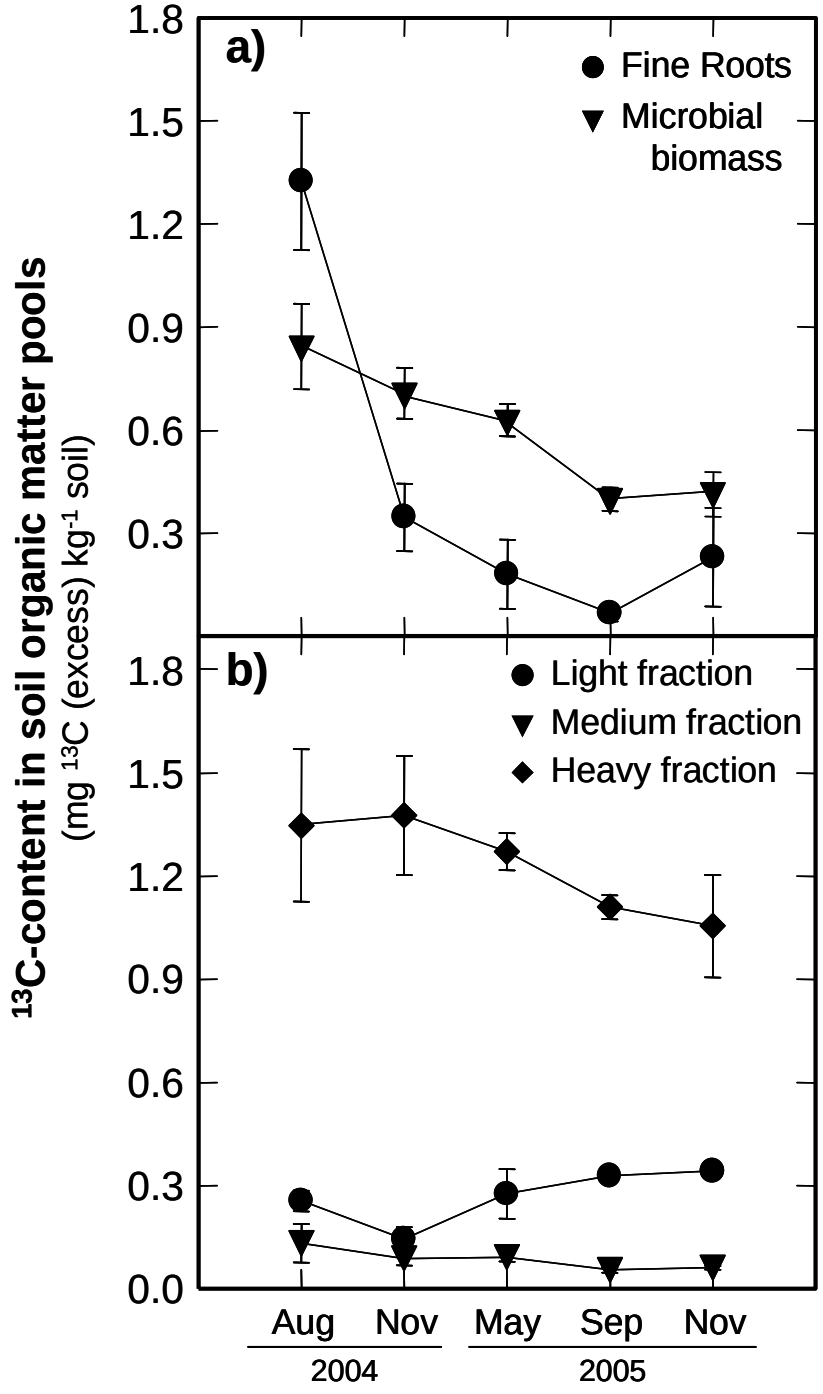

Figure 4-2. Change in distribution of ^{13}C (excess) among soil organic matter pools during 17 months of field incubation. ^{13}C-content derived from plant detritus in: (a) fine roots and microbial biomass, and (b) light, medium, and heavy fraction organic matter pools. Values shown are means (n=4 mesocosms) ± 1 s.e.

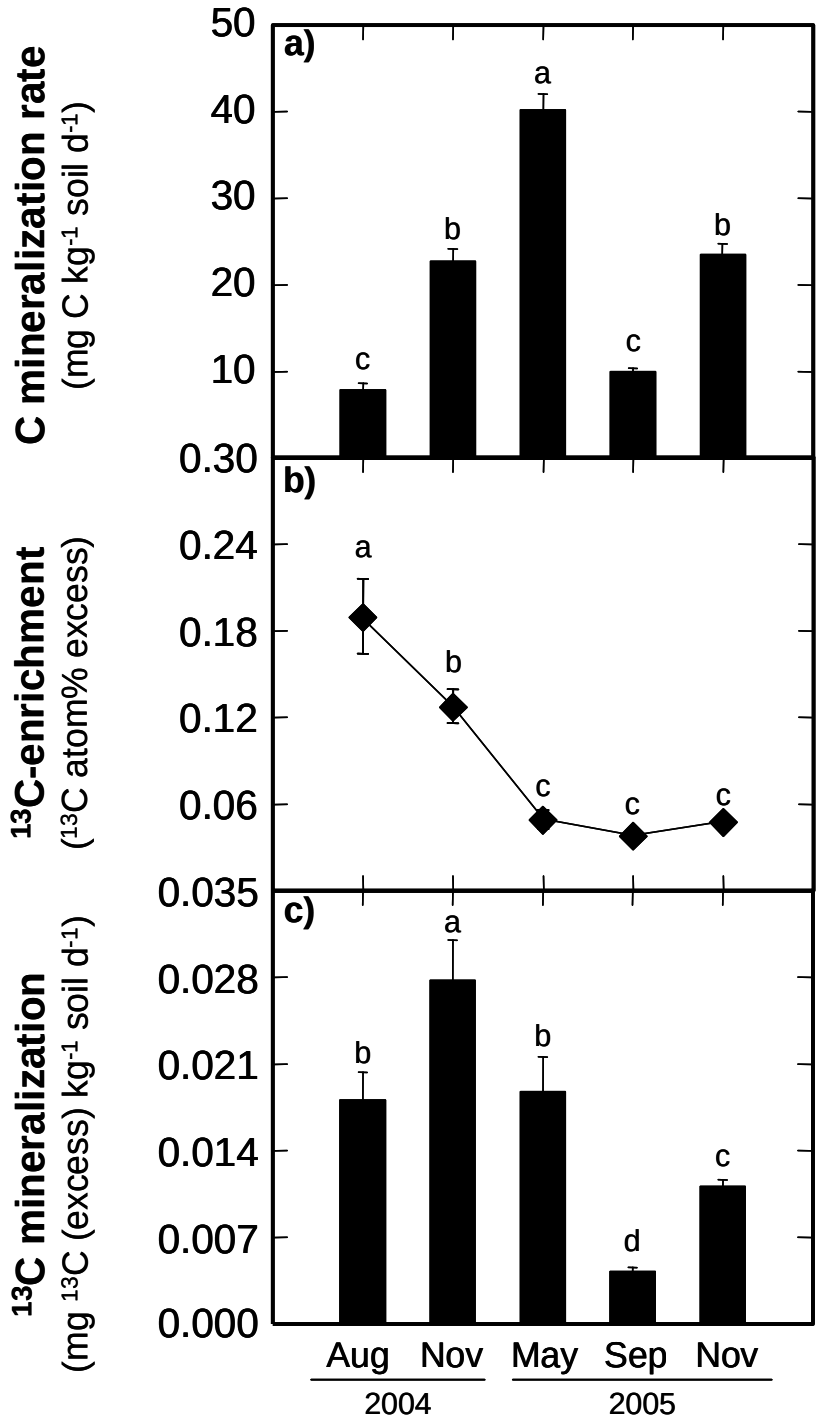

Figure 4-3. Seasonal variation in (a) rate, (b) ^{13}C-enrichment, and (c) ^{13}C-content of mineralized C during 48-h laboratory incubations. Error bars are standard error, may be smaller than symbol. Letters indicate significant differences among sampling dates.

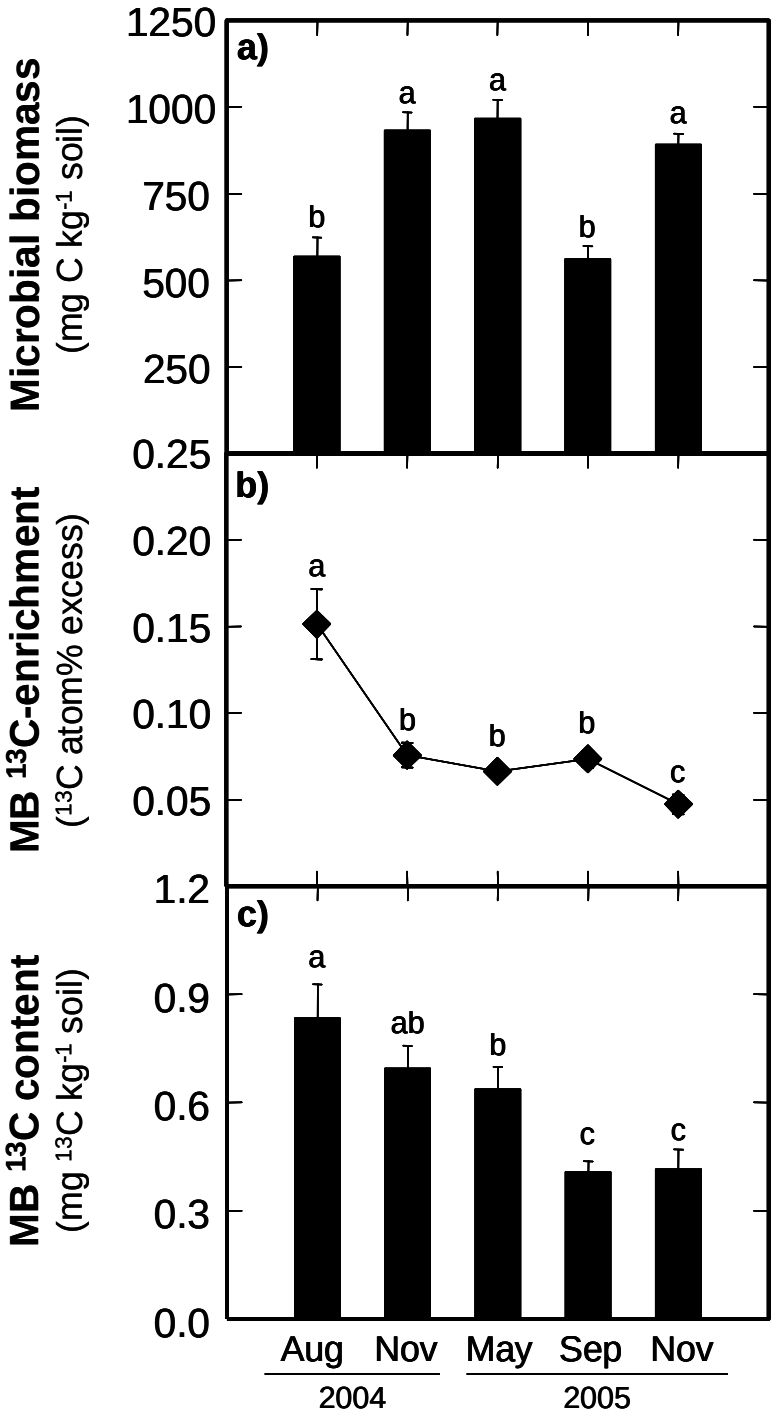

Figure 4-4. Seasonal variation in (a) microbial biomass-C, (b) microbial biomass ^{13}C-enrichment, and (c) microbial biomass ^{13}C-content. Letters indicate significant differences among sampling dates.

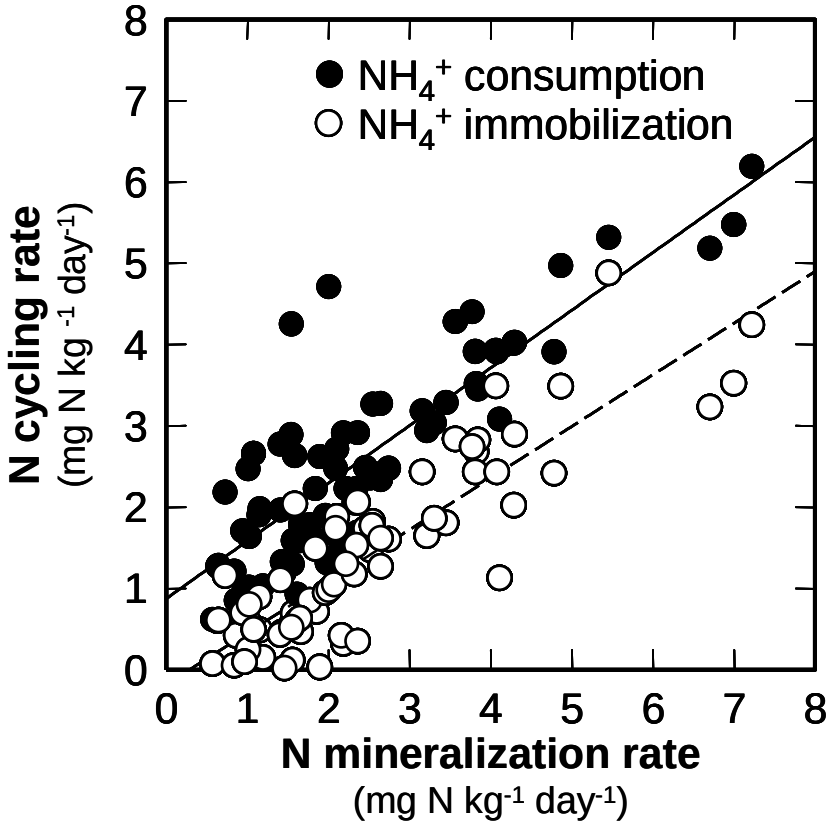

Figure 4-5. Gross rates of NH_4^+ consumption (black-filled circles) and NH_4^+ immobilization (white-filled circles) in relation to gross N mineralization rates across all sampling dates. Solid line represents linear regression for NH_4^+ consumption, and dashed line represents linear regression for NH_4^+ immobilization rates.

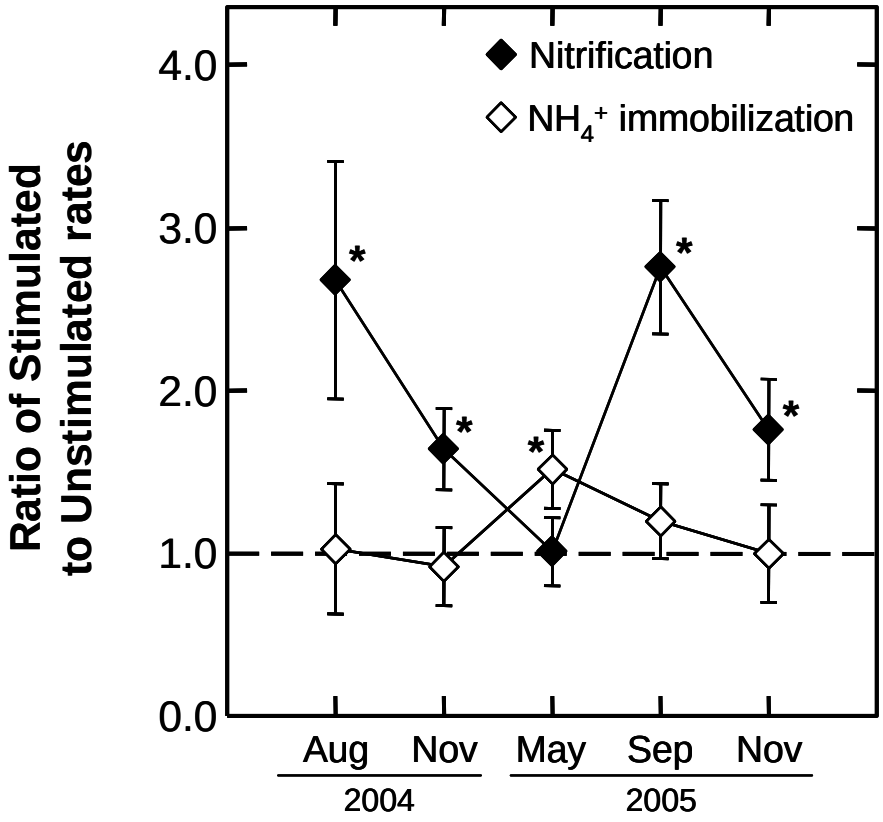

Figure 4-6. Relative effects of $^{15}NH_4^+$ addition on soil nitrification and NH_4^+ immobilization rates. Dashed line (1.0) indicates equivalent rates under stimulated and unstimulated conditions. Significant stimulation of NH_4^+ immobilization with $^{15}NH_4^+$ addition is considered strong evidence for an NH_4^+ limitation of heterotrophic microbial activity.

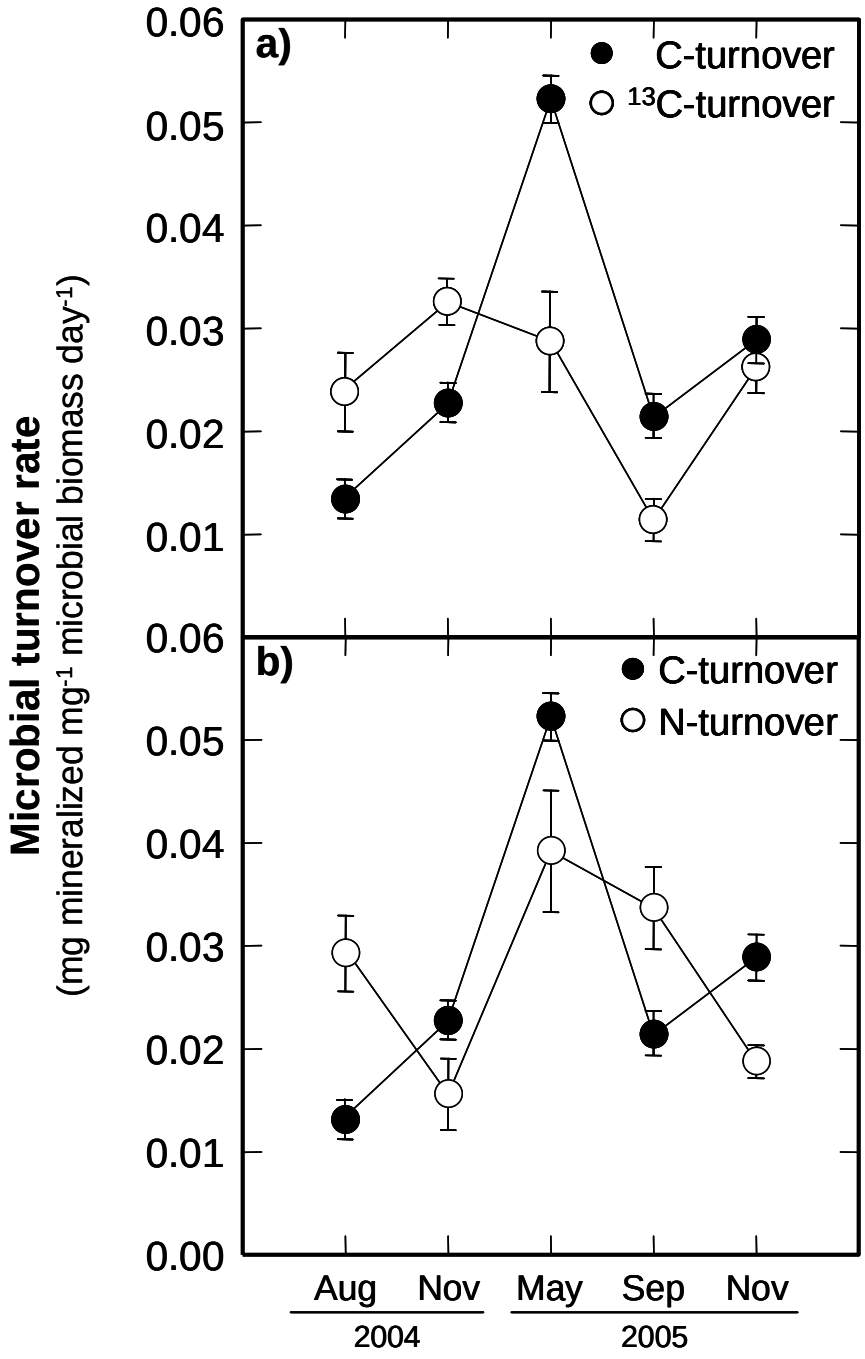

Figure 4-7. Seasonal variation in (a) microbial C- versus ^{13}C-turnover rates, and (b) microbial C- versus N-turnover rates, calculated as mineralization rate divided by microbial pool size. Error bars represent ± 1 s.e.

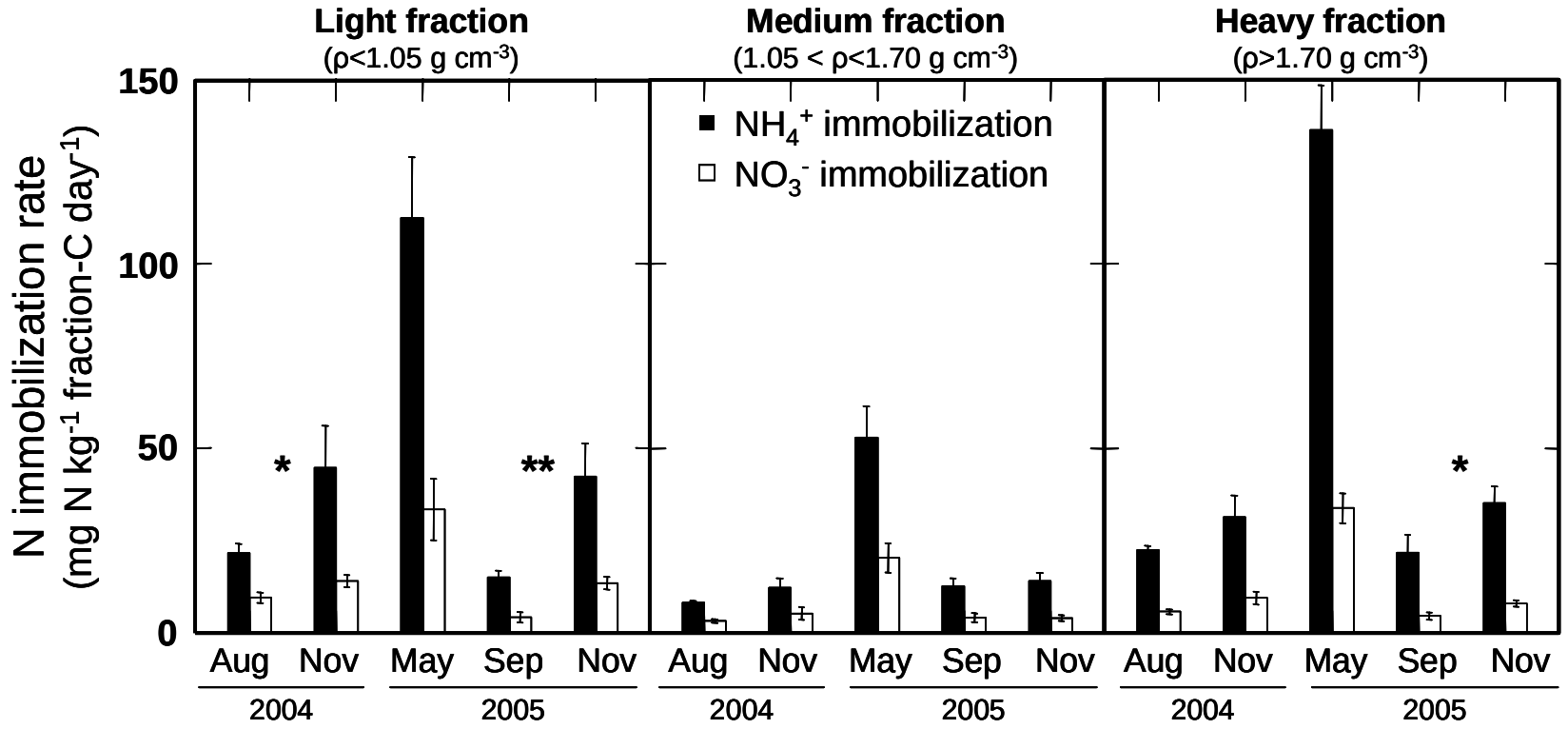

Figure 4-8. N immobilization associated with organic matter density fractions. Results show mean NH_4^+ and NO_3^- immobilization rates in light fraction, medium fraction, and heavy fraction organic matter during laboratory incubations. N immobilization rates were significantly greater in spring than summer and autumn for all organic matter fractions. Asterisks indicate a significant increase in N immobilization rate between summer and autumn (*, $p<0.05$; **, $p<0.005$).

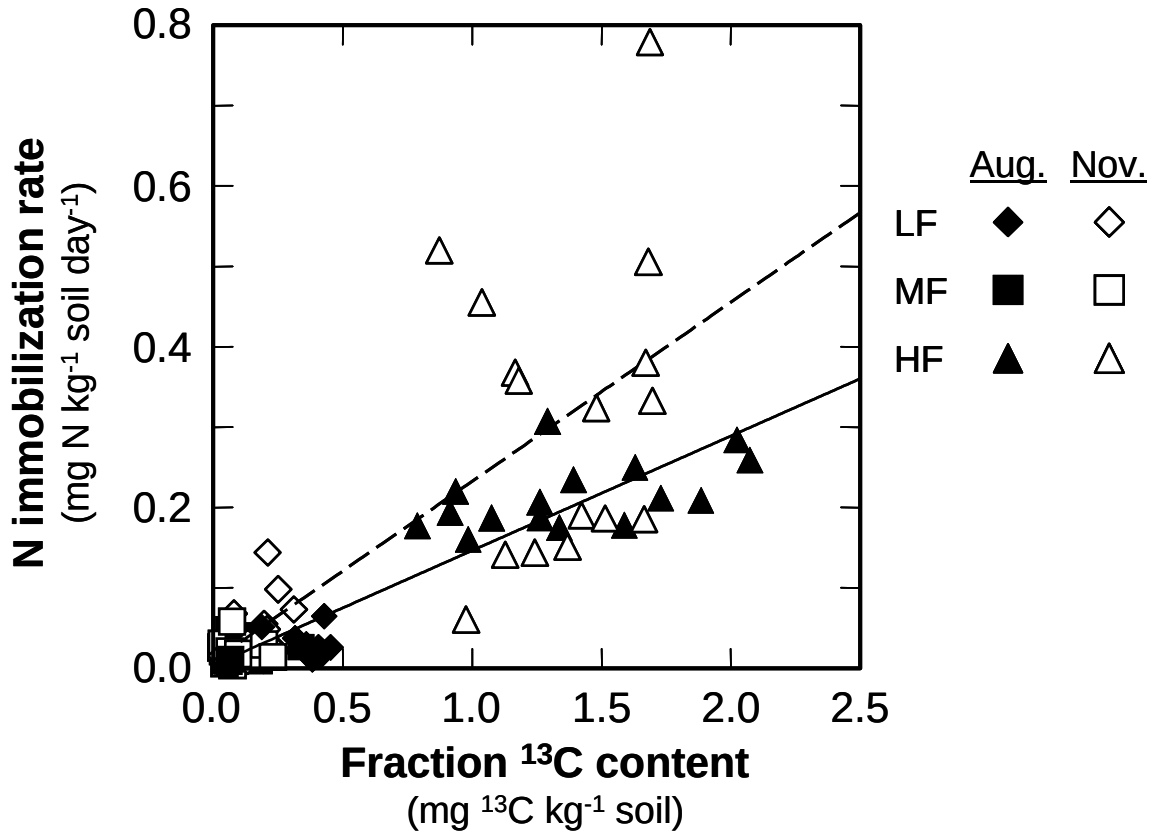

Figure 4-9. Organic matter fraction N immobilization rate versus fraction ^{13}C content from the first summer (black-filled symbols) and first autumn (white-filled symbols) sampling dates. Organic matter fractions with greatest ^{13}C content were positively correlated with highest N immobilization rates (r^2 = 0.66 and 0.80, for summer [August] and autumn [November], respectively). In addition, N immobilization rates per unit ^{13}C were greater in autumn than in summer, presumably due to higher soil moisture content in autumn.

CHAPTER 5

CONCLUSIONS AND DIRECTIONS FOR FUTURE WORK

Sagebrush-dominated rangelands comprise extensive land areas in the Great Basin and intermountain regions of the western U.S. (West and Young 2000), and these ecosystems are being substantially altered by grazing, rangeland improvement, exotic plant invasions, and altered wildfire regimes (Stewart and Hull 1949, D'Antonio and Vitousek 1992, West 1999, Bradley and Mustard 2005). These disturbances affect the composition and structure of native sagebrush vegetation, typically by causing a shift in dominance from shrubs to introduced perennial or invasive annual grasses (Stewart and Hull 1949, West 1999), and may significantly impact ecosystem C and N cycling in semiarid ecosystems. This is important because the magnitude of C cycling in terrestrial ecosystems, via plant primary production and microbial organic matter decomposition, is strongly linked to soil N dynamics. The two principal objectives of this research were first, to understand how shifts in the dominant vegetation of semiarid rangelands affect plant C and N cycling, and second, to examine the mechanisms that link soil C and N dynamics to ecosystem change.

The larger-scale consequences of vegetation change on C and N cycling in sagebrush-dominated ecosystems are likely to include direct losses of C and N from long-lived woody tissues as a result of rangeland management and wildfire (Bradley et al. 2006), however, rates of plant productivity – and thus rates of organic matter input to soils – may also differ between grass- and shrub-dominated ecosystems (Schlesinger et al. 1990, Huenneke et al. 2002, Ivans 2005, Prater et al. 2006). Results from my research

(reported in Chapter 2) provide evidence that differences in vegetation type have significant effects on the distribution of plant biomass C and N and the quantity of plant C and N inputs to soil. While sagebrush-dominated sites had greater C and N storage in plant biomass than perennial or annual grass systems (largely due to woody biomass accumulation), plant C and N inputs to soil were greatest in the annual grass-dominated system, contrary to my original hypothesis. This was largely due to differences in the distribution of aboveground and belowground biomass and to slower root turnover of perennial versus annual plants. Greater inputs of C and N in grass- versus sagebrush dominated sites may be responsible for the larger soil C and N pools observed in surface soils, and could eventually result in faster rates of soil C and N cycling in sites dominated invasive grasses compared to native sagebrush.

While differences in plant productivity among vegetation types were substantial, differences in rates of soil C and N cycling among vegetation types were more subtle (see Chapter 3 and 4). One of the most clear indications of differences in soil N cycling between sagebrush and annual grass-dominated vegetation types is the larger accumulation of NO_3^- during the summer dry-season in surface soils dominated by cheatgrass compared to perennial vegetation; this appears to be a common phenomenon in semiarid ecosystems (Booth et al. 2003, Sperry et al. 2006, Hooker et al. 2008; see also Chapter 2). Accumulation of NO_3^- in soil implies that microbial growth and activity are limited by the availability of C (substrate) rather than N (Hart et al. 1994, Chen and Stark 2000). Given that soils dominated by cheatgrass had greater inputs of plant detritus than soils dominated by sagebrush or crested wheatgrass (see Chapter 2), I proposed that differences in the timing of plant biomass turnover among vegetation types, relative to

the onset of the summer dry season, might explain why cheatgrass-dominated soils had both greater C inputs and greater summertime NO_3^- accumulation than native perennial-dominated soils. I hypothesized that microbial C limitation in the face of large pools of recently released plant detritus could be due to abiotic restrictions on microbial activity in dry soils, such that there is a time-lag in microbial utilization of plant detritus until after soil moisture increases in autumn.

In the first of two experiments, I examined whether earlier release of plant biomass to the soil detrital pool, prior to the summer dry-season, stimulated soil C availability and N immobilization rates (Chapter 3). Results from this study did not support the hypothesis, such that earlier inputs of plant detritus to soil stimulated soil N availability to a much greater degree than C availability, and resulted in soil NO_3^- pools that were 3-5 times greater than in untreated soils. It appears that the substrates consumed by soil microbes in response to earlier inputs of plant detritus had much lower C:N ratios than could have been predicted based on the C:N stoichiometry of plant foliage and root detritus.

In the second experiment, I examined whether microbial use of substrates derived from current year annual grass detritus versus older, more highly decomposed soil organic matter varied seasonally, and if so, how this variation affected microbial C and N dynamics (Chapter 4). I hypothesized that microbial consumption of recent detritus would increase between summer and autumn, as soil moisture increased after the summer dry season, and this would result in greater N immobilization rates. Results indicated that microbial consumption of recent detritus increased from summer to autumn, however, the relative contribution of recent detritus to total microbial C availability declined by 50%

during this same time period, and there was no apparent increase in gross N immobilization rates in bulk soils between summer and autumn. Thus, there is no clear evidence from this experiment for a time-lag in microbial colonization of recent detritus during summer.

In general, results from these two experiments suggest that microbial activity in the semiarid soils studied here was largely limited by the availability of C substrates, rather than N – even when rates of decomposition and soil C cycling were rapid. Interestingly, soil microbial activity appears to be N-limited only when plants were actively growing (see Chapter 4, Figure 4-6). Competition between plant roots and soil microbes for available nutrients may be an important limitation on rates of plant growth during the growing season (Field and Mooney 1986), however, it remains unclear how much of this is due to direct competition for available N as opposed to stimulation of microbial growth (and N immobilization rates) from plant rhizodeposition of labile C. Nonetheless, rapid turnover of microbial C and N in soils with actively growing plants (see Figure 4-7) appears to result in tight plant-microbe-soil linkages. Interruption of plant activity during the growing season – due to senescence of cool-season annual vegetation or other soil disturbances – results in the loss of mineralized soil organic C and N, and may serve as a positive feedback for further expansion of noxious invasive vegetation, especially since invasive annual grasses tend to out compete native perennial vegetation at elevated levels of nutrient availability (Monaco et al. 2003, Vasquez et al. 2008).

A large component of this research has been focused on the distinction between plant detrital inputs to soil versus older more highly decomposed soil organic matter

(*sensu stricto*) associated with soil minerals, and how these organic matter sources affect microbial C and N dynamics. Soil organic matter is exceptionally heterogeneous with respect to the age, chemical structure, biological availability and C:N stoichiometry of its constituents (Kogel-Knaber 2002, Gregorich et al. 2006, von Lutzow et al. 2007). Recent work has conceptually incorporated this variation into two comparatively distinct microsites as habitats for microbial growth (see Schimel and Bennett 2004). Soil microbes are thought to be distributed among distinct microsites dominated by N-rich (C-limited) and C-rich (N-limited) substrates, based on the simultaneous occurrence of opposing N mineralization and N immobilization processes in bulk soils (Chen and Stark 2000). Under this conceptual model, the source of mineralizable N is derived predominantly from older, more highly decomposed mineral-associated organic matter with narrow C:N ratios, such as the heavy fraction (HF). High rates of microbial N consumption are expected in C-rich microsites, and associated with particulate organic matter derived from plant detritus, such as light fraction (LF) (Sollins et al. 1984, Boone 1994, Whalen et al. 2000).

A notable result from this dissertation research is derived from the examination of microbial activity associated with soil organic matter density fractions. In two separate studies, I found that microbial activity (assessed as N immobilization rate) associated with both light and heavy organic matter fractions were responsive to changes in the quantity and timing of plant detrital inputs (Chapter 3), and were sensitive to seasonal variation in environmental conditions and soil C availability (Chapter 4). A few other studies have found LF organic matter to be a significant sink for immobilized N (Recous et al. 1999, Whalen et al. 2001, Compton and Boone 2002). Microbial activity and N

immobilization associated with particulate LF organic matter is consistent with microbial growth on recently released plant detritus. I also observed that the HF was a rapid and persistent sink for labile C that is actively cycled through the microbial biomass. High rates of N immobilization and rapid C sequestration associated with HF were unexpected, since HF has narrow C:N ratios and was generally thought to be a source of inorganic N rather than a sink (Boone 1994, Whalen et al. 2000). These results provide support for recent work suggesting that at least a portion of C in HF is relatively labile (see Swanston et al. 2002, 2005, Crow et al. 2006), and not as recalcitrant as formerly thought.

Based on the results from Chapters 3 and 4, it appears that sequestration and turnover of C and N among distinct soil organic matter fractions occurs rapidly in the semiarid soils studied in this research. While it was difficult to establish clear linkages between microbial consumption of recently released plant detritus and bulk soil N dynamics (see Chapter 4), this could be due to differences in the C and N dynamics of soil microbial communities associated with distinct soil organic matter fractions. These differences may be controlled by the C:N stoichiometry of microbially available substrates, or may reflect differences in microbial community composition and structure. Tracking the fate and turnover of C and N among distinct organic matter fractions may increase our ability to detect subtle changes in soil C and N dynamics at spatial scales that more closely match the processes involved. In order to gain a better understanding of the controls on the sequestration of recently released C and the retention of older organic matter in soils, future work should aim to characterize the microbial communities and the C and N dynamics associated within distinct microsites of soil organic matter.

Results from the three data-chapters in this dissertation (Chapters 2, 3, and 4) also point to the potential for severe consequences on ecosystem C and N dynamics in semiarid rangelands in response to future climatic change, especially if future climate change scenarios involving shifts in the seasonality of growing season precipitation are borne out (see Christensen et al. 2007). For example, if the probability of intense summer precipitation events increases in the northern Great Basin (via a northward shift in monsoonal rains; Schlesinger and Mitchell 1987, Mitchell et al. 1990), then microbial activity in response to precipitation pulses in soils dominated by recently senesced cheatgrass could result in rapid decomposition of cheatgrass detritus and the accumulation of large pools of inorganic N in surface soils. Insofar as invasive plants are more competitive than native vegetation at elevated levels of nutrient availability (Monaco et al. 2003, Vasquez et al. 2008), this could increase the rate of invasive species colonization and dominance of semiarid rangelands. In addition, large inorganic N pools and rapid rates of N mineralization could also give rise to elevated rates of nutrient loss – via overland flow, NO_3^- leaching below the rooting zone, and trace gas emissions (Peterjohn and Schlesinger 1990, Smart et al. 1999, Stark et al. 2002, Schaeffer et al. 2003, Walvoord et al. 2003, Jackson et al. 2004, Schaeffer and Evans 2005, Lewis et al. 2006). Subsequently, the seasonal increase in nutrient availability would allow for greater ecosystem N losses over time, possibly leading to soil desertification (sensu Schlesinger et al. 1990).

Some directions for future research

As is the case for most scientific endeavors, the research in this dissertation produced a greater abundance of questions than answers. I propose some general directions for future research based on my work below.

- *What are the consequences of vegetation change on net ecosystem production?*

  After a shift in dominant vegetation in semiarid ecosystems, for example cheatgrass invasion and dominance of sagebrush stands, how do patterns of ecosystem C and N cycling vary over successional time-scales? How does the potential increase in wildfire frequency and severity associated with cheatgrass invasion affect ecosystem C and N balance relative to intact sagebrush systems over the long-term?

- *What are the consequences of vegetation change on the magnitude and mechanisms of ecosystem C and N loss?*

  How do changes in the timing of plant activity and in the quantity of plant C and N inputs to soil after a shift in vegetation type affect rates of nutrient loss via trace gas (NH_3, NO and N_2O) flux and leaching (NO_3^-) losses below the root zone? What are the impacts of contemporary shifts in semiarid vegetation on nutrient flux in deep soils and nutrient accumulation in near-surface groundwaters?

- What controls the availability of soil organic matter as substrates for microbial growth in semiarid soils?

While mineral-associated soil organic matter, recent particulate detritus, and root exudates are important sources of microbially available substrates, how does microbial consumption of these substrates affect microbial growth and soil N availability? Is the production and consumption of substrates from these disparate organic matter sources regulated by distinct microbial communities?

Future changes in global climate, as well as continuing impacts from intensification of land use practices and exotic plant invasions, are likely to have profound impacts on the composition and structure of semiarid plant communities in the Great Basin. Since the dynamics of vegetation change in semiarid ecosystems are inextricably linked to soil C and N cycling, greater understanding of biogeochemical C and N cycles will improve our ability to predict the consequences of these impacts.

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APPENDICES

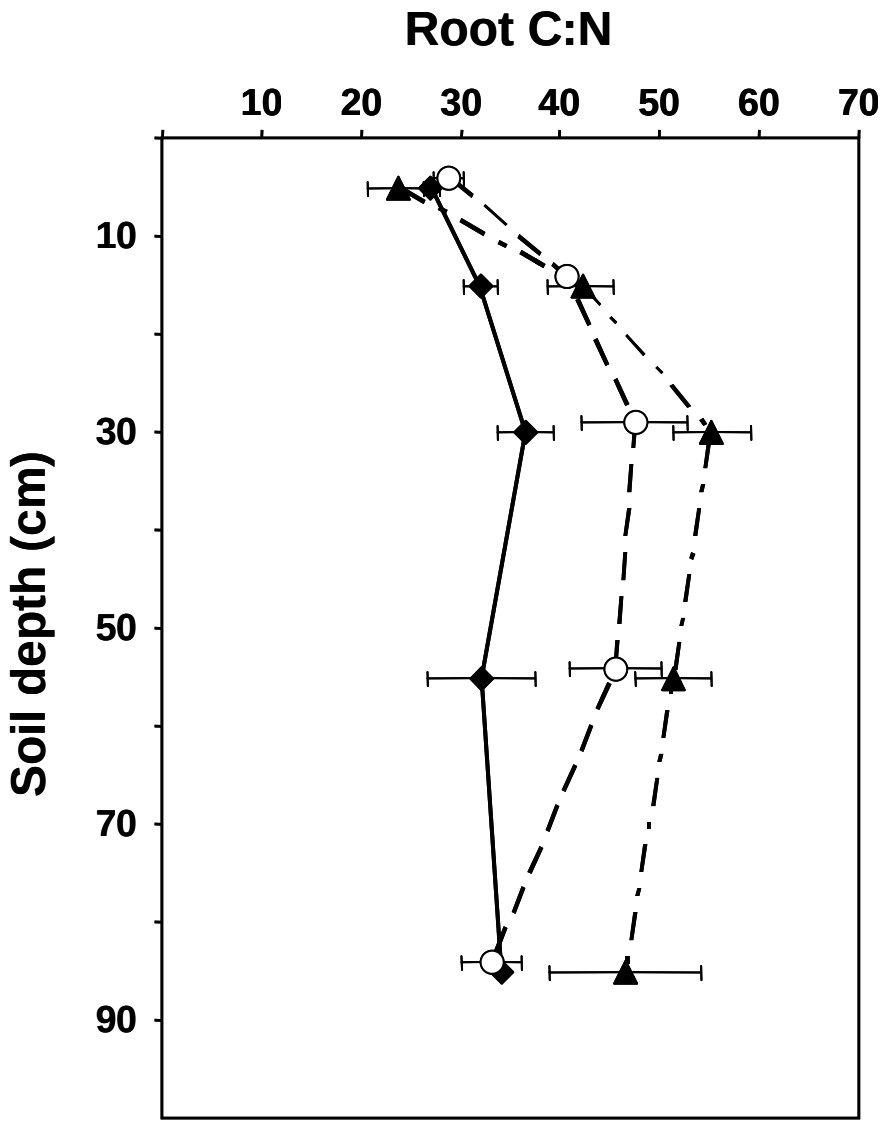

Figure A-1. Root C:N ratios with soil depth among three vegetation types. Symbols: cheatgrass (solid diamonds), crested wheatgrass (circles), sagebrush-canopy (solid triangles). Error bars represent $\pm$1 standard error (n = 4). Symbols adjusted along the vertical (soil depth) axis for clarity.

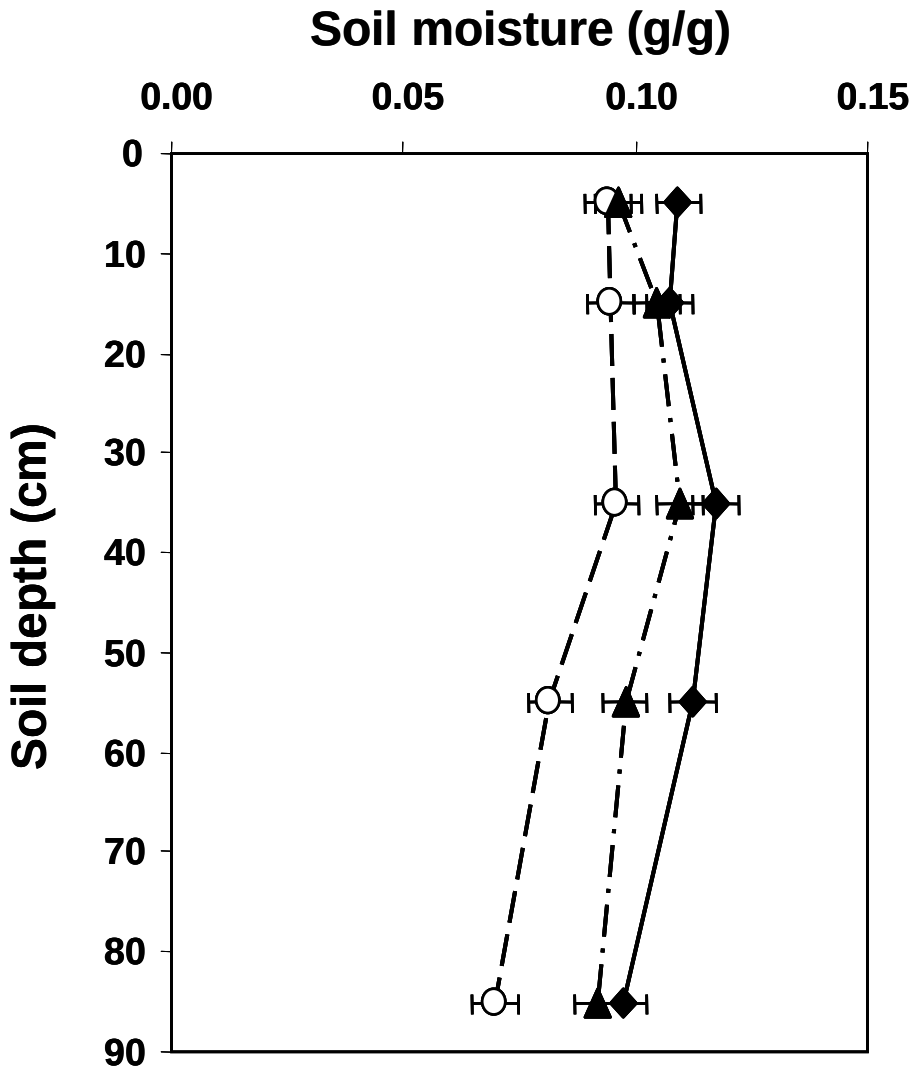

Figure A-2. Mean soil gravimetric moisture content with soil depth among three vegetation types. Symbols: cheatgrass (solid diamonds), crested wheatgrass (circles), sagebrush-canopy (solid triangles). Error bars represent $\pm$1 standard error (n = 4). Note that for soils beneath 20 cm depth, soil moisture content was significantly greater beneath cheatgrass than crested wheatgrass vegetation types ($p<0.01$), and sagebrush was intermediate.

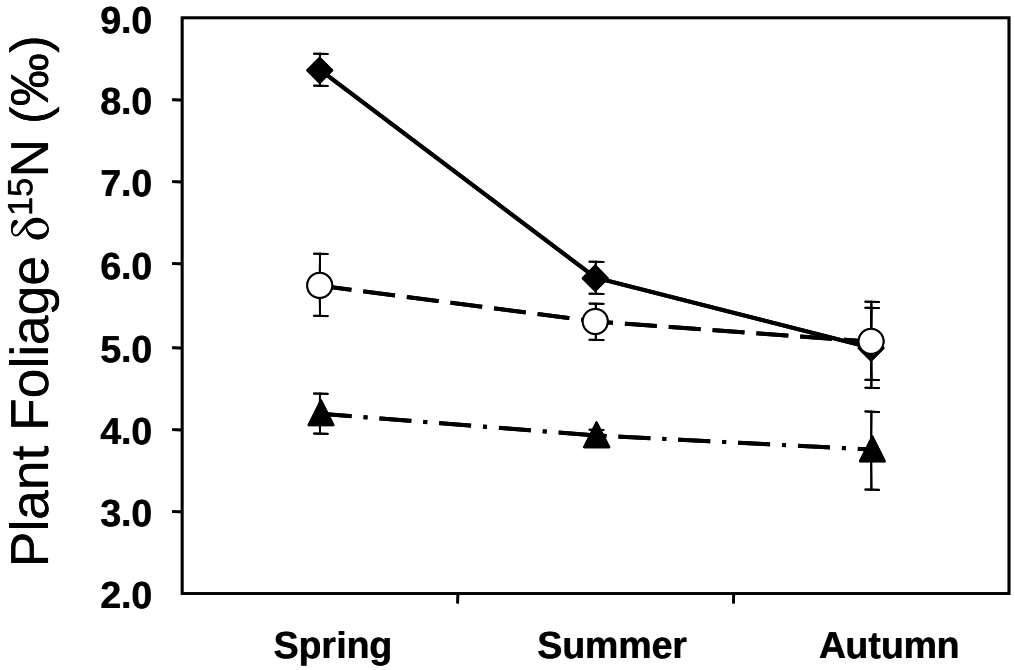

Figure A-3. Seasonal variation in foliar $\delta^{15}N$ signatures among three vegetation types. Symbols: cheatgrass (solid diamonds), crested wheatgrass (circles), sagebrush-canopy (solid triangles). Error bars represent $\pm$1 standard error (n = 4).

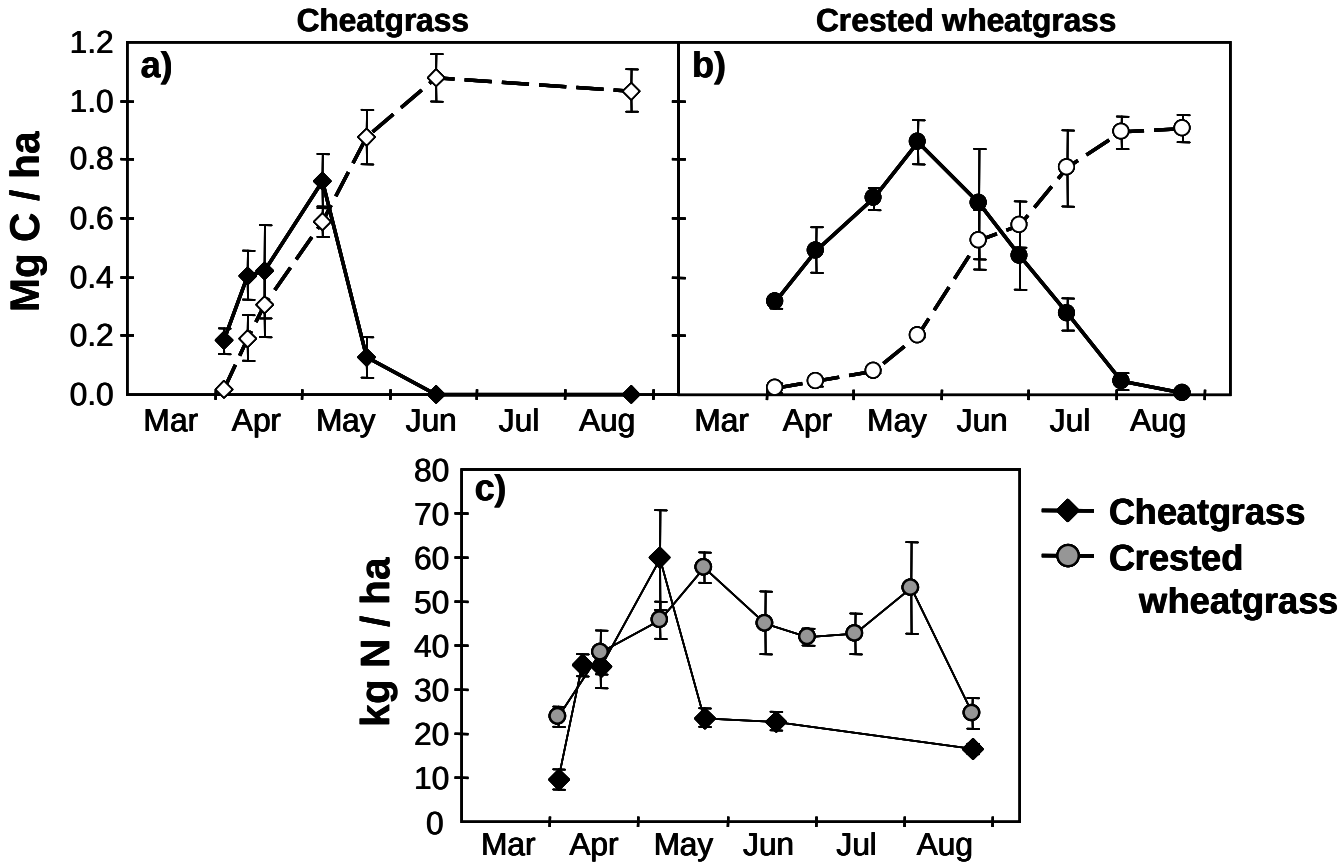

Figure A-4. Plant aboveground biomass C and N content over time. Live (solid black) and dead (white-filled) C content of (a) Cheatgrass, and (b) Crested wheatgrass during the spring-summer growing season. (c) Total aboveground N content (live and dead) for cheatgrass (diamonds) and crested wheatgrass (circles). Error bars represent $\pm$1 standard error (n = 4).

Appendix A-5 Co-author approval forms for Chapter 2

23 March, 2009

Dr. A. Joshua Leffler
Department of Wildland Resources
5230 Old Main Hill
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Logan, UT 84322-5230

Dear Josh,

I am in the process of finalizing my Dissertation in the Department of Biology at Utah State University, and will complete this work in Spring semester of 2009.

As a coauthor on the manuscript "Distribution of ecosystem C and N within contrasting vegetation types in a semiarid rangeland in the Great Basin, USA" published in *Biogeochemistry*, I am requesting your permission to include this work as part of my Dissertation. I will be sure to include proper citations to this work, and copyright and reprint rights information in a appendix, as required.

Please indicate your approval of this request by signing in the space provided, attaching any other form or instruction necessary to confirm permission. If you have any questions, please feel free to contact me.

I look forward to your prompt reply.

Thank you for your cooperation,

Toby D. Hooker

I hereby give permission to Toby Hooker to reprint the following material in his Dissertation.

Hooker, T. D., J. M. Stark, U. Norton, A. J. Leffler, M. Peek, and R. Ryel. 2008. Distribution of ecosystem C and N within contrasting vegetation types in a semiarid rangeland in the Great Basin, USA. Biogeochemistry 90:291-308.

Fee: _____

Signed: _____

23 March, 2009

Dr. Urszula Norton
Renewable Resources Department
1000 E. University Avenue
University of Wyoming
Laramie, WY 82071-3354

Dear Urszula,

I am in the process of finalizing my Dissertation in the Department of Biology at Utah State University, and will complete this work in Spring semester of 2009.

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Fee: _____

Signed: _____

23 March, 2009

Dr. Michael S. Peek
Department of Biology
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Dear Mike,

I am in the process of finalizing my Dissertation in the Department of Biology at Utah State University, and will complete this work in Spring semester of 2009.

As a coauthor on the manuscript "Distribution of ecosystem C and N within contrasting vegetation types in a semiarid rangeland in the Great Basin, USA" published in *Biogeochemistry*, I am requesting your permission to include this work as part of my Dissertation. I will be sure to include proper citations to this work, and copyright and reprint rights information in a appendix, as required.

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I look forward to your prompt reply.

Thank you for your cooperation,

Toby D. Hooker

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Fee: None

Signed: Michael S Peek

23 March, 2009

Dr. Ronald J. Ryel
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Dear Ron,

I am in the process of finalizing my Dissertation in the Department of Biology at Utah State University, and will complete this work in Spring semester of 2009.

As a coauthor on the manuscript "Distribution of ecosystem C and N within contrasting vegetation types in a semiarid rangeland in the Great Basin, USA" published in *Biogeochemistry*, I am requesting your permission to include this work as part of my Dissertation. I will be sure to include proper citations to this work, and copyright and reprint rights information in a appendix, as required.

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Thank you for your cooperation,

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Signed: 

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Hooker, T.D., J.M. Stark, U. Norton, A.J. Leffler, M. Peek, and R. Ryel. 2008. Distribution of ecosystem C and N within contrasting vegetation types in a semiarid rangeland in the Great Basin, USA. Biogeochemistry 90: 291-308.

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VITAE (continued)

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